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A CATALOGUE

OF THE

MESOZOIC MAMMALIA

IN THE GEOLOGICAL DEPARTMENT OF THE BRITISH MUSEUM

BY

GEORGE GAYLORD SIMPSON, PH.D.

ASSISTANT CURATOR OF FOSSIL MAMMALS IN THE AMERICAN MUSEUM OF NATURAL HISTORY, NEW YORK

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PREFACE

In 1926 Dr. Gaylord Simpson came to Europe from Yale University, as holder of a National Research Fellowship in the Biological Sciences, granted by the National Research Council of the United States of America, with the intention of studying the remains of Mesozoic Mammalia. Since by far the more important of those remains on this side of the Atlantic are preserved in the Geological Department of the British Museum, advantage was taken of this visit to request Dr. Simpson to prepare a Catalogue for publication by the Trustees. The work thus produced by so competent an authority needs no recommendation, but I must thank Dr. Simpson for having so readily undertaken the task, and thus giving us the benefit of his training and experience.

For the preparation of this Catalogue Dr. Simpson visited several other museums in England and on the Continent, and desires his thanks to be recorded here, along with our own, to the many colleagues who have thus aided his work. Chief among these are: Dr. F. L. Kitchin, palaeontologist to the Geological Survey, who permitted the study of the holotype of *Stereognathus ooliticus* and Willett's specimen of *Triconodon mordax;* Prof. E. S. Goodrich, F.R.S., who allowed examination of the valuable specimens from Stonesfield in the Oxford University Museum; Dr. P. E. Martineau, Hon. Secretary of the Bath Royal Literary and Scientific Institution, who gave access to the Moore Collection, including all Owen's type-material of *Microcleptes moorei;* Dr. W. E. Collinge, Keeper of the Yorkshire Museum, who facilitated the study of the type-specimens of *Amphilestes broderipi;* Professor E. Hennig and Professor F. von Huene, of Tübingen, who kindly put the material of *Oligokyphus* at the author's service; and Dr. F. Berckheimer, of the Naturaliensammlung, Stuttgart, who gave similar facilities in respect to *Plieningeria antiqua*, "*Stathmodon*," and "Plienger's larger specimen." Valuable suggestions on certain points have been offered by Prof. G. Elliot Smith, F.R.S., Prof. D. M. S. Watson, F.R.S., and Prof. W. D. Matthew, F.R.S.

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In his Introduction Dr. Simpson has himself thanked Mr. A. T. Hopwood, Assistant in the Department of Geology, but, as Editor, I have also to thank him warmly for his unwearied help in checking references and seeing the sheets through

the press. It is right to add that this task was placed unreservedly in our hands by Dr. Simpson, who, immediately the manuscript was ready, returned to New York to take up an appointment in the Department of Vertebrate Palaeontology at the American Museum of Natural History.

The details of the papers referred to (by Author's name and date) throughout the memoir are given on page 203. The contractions of periodicals follow, in the main, the World List of Scientific Periodicals.

F. A. BATHER.

Department of Geology,
British Museum (Natural History).
10th February, 1928.

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CATALOGUE OF MESOZOIC MAMMALIA

INTRODUCTION

THE history of mammalian life in the Cainozoic, the so-called "Age of Mammals," has occupied the attention of several generations of paleontologists. Great collections have been brought together from all parts of the world, and however many gaps remain to be filled, at least the broader lines of mammalian evolution during this era are now well understood. Few, however, stop to realize that, even were Cainozoic history completely known, only a fraction of the evolution of the Class Mammalia would be made clear. The mammals were already well advanced at the beginning of the Eocene: it has been estimated that two-thirds of their total development from the reptilian to the recent mammalian type had already taken place by the end of the Mesozoic. This lost two-thirds, this mammalian prehistory, is much more basic in character than the relatively minor differentiation which took place in the Cainozoic. It must contain the answers to the most fundamental problems of mammalian classification and phylogeny, to which later mammals, taken by themselves, always and inevitably yield only equivocal, misleading, or incomplete clues.

Only the Mesozoic mammals can cast direct light on these basic early stages, but they have long been either neglected or clouded by misinterpretation or erroneous observation. The reason for this condition of affairs is, however, not far to seek. The remains of Mesozoic mammals are among the smallest, the rarest, and the most fragile of fossils. Very few students have been able to make any considerable first-hand study of them; the last general review of the subject was made just forty years ago. Binocular microscopes were not then available, knowledge of other mammals, especially of fossil mammals, was much less complete than now, and, most important of all, no one had been enabled to study both American and European forms and to make adequate syntheses and comparisons. Some of these disabilities can now be removed.

Of the remains of Mesozoic mammals, only the more precious for their great scarcity, a very considerable number is in the British Museum (Natural History). Here is *Tritylodon*, the oldest known mammal skull; here is one of the two original jaws brought to light by Broderip and studied by Cuvier; here, with one exception, is the entire priceless Purbeck collection; here are all the known Lower Cretaceous mammals; here, too, are other invaluable representative specimens from the Rhaetic rocks, the Stonesfield Slate, and the Upper Cretaceous formations.

It is upon this classic collection, which will always remain the fundamental basis for the study of Mesozoic Mammalia, that the present monograph is based. All the other still extant material of European Mesozoic mammals has, however, also been studied and is included. For the Triassic forms the collections at Stuttgart, Tübingen, Bath, and Yale University have been drawn on, in addition to that of the British Museum. The Stonesfield specimens are in the Oxford, York, Museum of Practical Geology, and British Museum collections. One Purbeck jaw is in the Museum of Practical Geology. Far the greater number of all the specimens known are in the Beckles collection from the Purbeck beds, purchased by the British Museum in 1876.

In addition to the acknowledgments made in the preface, the author wishes especially to thank Dr. F. A. Bather and Mr. A. T. Hopwood, who have placed the British Museum collection and every facility for its study at his disposal, and who have constantly assisted and encouraged the progress of the work.

PREVIOUS WORK

One of the first and one of the most dogmatic of great generalizations enunciated as the significance of fossil remains began to be fully appreciated was that "in the Secondary there occur no mammals." Yet this generalization was untrue, and the contradictory evidence was not long in forthcoming.

The first Mesozoic mammal to be found was obtained from Joshua Platt about 1764 by Sir Christopher Sykes. The unique importance of the specimen was not realized, else Sir Christopher might have anticipated Buckland by sixty years. The specimen passed into the collection of the Reverend C. Sykes, where it was found by Professor Phillips in 1828, and through the mediation of the latter it was presented to the museum of the Yorkshire Philosophical Society, where it still remains. It was later made the type of *Amphilestes broderipii* (Owen, 1871, p. 15).

The real discovery of Mesozoic mammals, that which was followed by the first appreciation of their significance, came about through the agency of William John Broderip, an amateur naturalist who spent the greater part of his long life as a Metropolitan Police magistrate, but who found time to pursue extended studies in natural history and to inspire others to do likewise. In 1812 the young Broderip was studying law at Oxford and also attending lectures under Professor Buckland. It was in this year (or perhaps in 1814, as Goodrich supposes) that, in the words of Broderip himself, " . . . an ancient stonemason, living at Heddington, who used to collect for me, made his appearance in my rooms at Oxford with two specimens of the lower jaws of mammiferous animals, imbedded in Stonesfield slate, fresh from the quarry. One of the jaws was purchased by my friend Professor Buckland, who exclaimed against my retaining both, and the other I lent to him some time ago" (Broderip, 1828).

Buckland and Broderip were equally convinced of the mammalian character of the remains thus acquired. The Stonesfield Slate, however, belongs to the lower oolites (Middle Jurassic) and hence is vastly older than any of the mammal-bearing strata which had hitherto been made known. Consequently, with commendable caution, they hesitated to announce their discovery. In 1818, however, the illustrious founder of the science of vertebrate palaeontology visited Oxford and saw the specimens. Cuvier assured Professor Buckland that they were indeed mammalian, and not unlike the jaws of an opossum.

Even thus encouraged, it was not until 1824 (not 1823 as stated by Owen and most writers subsequent to him) that the discovery was announced. In his "Memoir on the *Megalosaurus*" Buckland mentions these two jaws, referring them to the same family as the opossum "on the authority of M. Cuvier, who has examined [them]." In the following year Prévost, who had spent some time in England, published a

paper on the Stonesfield Slate in which he included the first detailed description and figure of Buckland's specimen, calling it " un mammifère carnassier insectivore qui pouvait offrir quelque analogie avec les Didelphes, mais qui appartiendrait à un genre inconnu." He also provided Cuvier with detailed drawings, so that the latter refers to the matter in the third edition of the " Ossemens fossiles " (1825) saying of the jaws that they, " lors d'une inspection rapide que j'en pris à Oxford, en 1818, me semblèrent de quelque Didelphe," and adding on the authority of Prévost's drawings that, while the jaws closely resemble those of the opossum, they have a higher number of cheek teeth than any other known ferine (" carnassier ").

The discovery thus made public created a veritable sensation among palaeontologists, and many were eager to attack it and to defend the generalization which it violated. The first question, as to the geological age of the enclosing beds, was met by Dr. Fitton (1828), with a detailed study which left no room for doubt. Since, then, the jaws were really of Oolitic age, it followed in the minds of many that they could not be mammalian, but must be reptilian, or even piscine. Agassiz, in a short note published in 1835, considered that the remains were too fragmentary for the determination of so important a question. In the following year Buckland, in his famous Bridgewater Treatise, reaffirmed the discovery and gave figures, the first save those of Prévost. De Blainville, basing himself on these figures of Buckland's, published in 1838 his " Doutes sur le prétendu Didelphe de Stonesfield," in which he proposed to do away with these doubts of his by affirming the reptilian nature of the jaw. He emphasized Cuvier's acceptance as reptilian of another jaw which had been supposed to belong to the same creature. In common with several other critics, de Blainville mistook the internal (" mylohyoid " or " meckelian ") groove for a suture, and believed that it demonstrated the compound, and therefore reptilian, nature of the lower jaw. To signalize the ambiguous nature of the material and to remove it from the genus *Didelphis*, de Blainville proposed the name *Amphitherium* for Buckland's specimen.

In order that the French critics might be convinced by seeing, Buckland took his specimen and a new one of the same species to Paris in the same year (1838). So far as de Blainville was concerned, this expedition was a total failure, as he left for the country the very day of Buckland's arrival, and did not see the specimens. This did not deter him from publishing very shortly thereafter (1838) " Nouveaux Doutes," in which he reasserted his belief in the saurian nature of the remains. Buckland did, however, make converts of those who actually saw the originals. Valenciennes published, in September, 1838, a paper in the *Comptes Rendus* in which he confirmed the opinion of Cuvier and Prévost and proposed the name *Thylacotherium prevostii*. In the same volume of the *Comptes Rendus* appeared notes by Duméril and by Geoffroy St. Hilaire in which those able naturalists also supported Cuvier's judgment.

If opinion was thus divided among the French savants, it was not less so in England. In December, 1838, Ogilby published his allegiance to the de Blainville banner, and he was closely followed by Grant in his article on extinct animals in *Thompson's British Annual* for 1839.

Only one man in England had the knowledge and prestige necessary to settle this question. On his return to England Buckland entrusted his specimens to Richard Owen. The latter at once (1838) published two papers in the *Transactions of the Geological Society*, followed in 1842 by a memoir on the Stonesfield fauna in which he discussed and figured not only the specimens of Buckland and Broderip but also some others. These publications mark the end of the controversy which had stirred scientific circles for some fifteen years. Owen showed that the supposed suture was a groove with an entire bottom, and pointed out the numerous other features which prove the mammalian character of the forms now known as *Amphitherium*, *Phascolotherium*, and *Amphilestes*. Since 1839 no one has denied the existence of Mesozoic mammals.

Before turning to other discoveries it is interesting to follow the later history of the Stonesfield mammalian fauna. Owen again referred to it in his "History of British Fossil Mammals and Birds" (1846) and his "Odontography" (1840–45). In 1854 Edward Charlesworth announced that there was in the possession of the Rev. J. Dennis, of Bury, a specimen from Stonesfield representing a fourth genus, *Stereognathus*. This specimen was also in due time submitted to Owen, who published a full account of it in 1857. Owen's final summing up of this fauna is included in his memoir of 1871, which is mentioned again below. Osborn reviewed the fauna in 1888 and added a fifth genus, *Amphitylus*, which, however, has not been generally accepted. Another note by him in the same year adds some points in regard to specimens which had not been seen when the larger work was written. It remained for Goodrich to make a definitive morphologic revision of this small but important fauna in 1894 in his admirable "Fossil Mammalia from the Stonesfield Slate."

Another field must now be considered. In 1847 Professor Plieninger, of Stuttgart, was carefully sifting the sand of a bone bed in the Rhaetic of Württemberg. The result of this labour was "eine ungeheure Masse von Zähnen, Schuppen, Coprolithen und unkenntlichen Skelettheilen von Fischen und Sauriern." The diligent professor examined all of this mass with a hand lens and was rewarded with what were then the oldest known mammals. On a single tooth he erected the genus and species *Microlestes antiquus* [=*Thomasia antiqua*]—a form now generally, but perhaps erroneously, referred to the Multituberculata.

This prime discovery was followed in 1854 by another of even greater importance. In that year the Rev. P. B. Brodie and Mr. Wilcox, of Swanage, Dorset, sent to Owen a lot of small fossils from the Purbeck beds of Durdlestone Bay, near Swanage, on the Isle of Purbeck. The majority of these specimens were described as lacertians, but some of the jaws proved to be mammalian. The result was the establishment in the same year of the genus *Spalacotherium*, first known member of the vitally important Purbeckian (uppermost Jurassic) mammalian fauna of England. This discovery greatly stimulated interest in the subject and S. H. Beckles carried on extensive explorations in the sea cliff at Durdlestone Bay for many years, his efforts resulting in a fine collection now in the British Museum. Basing his work on the Beckles Collection, Falconer published in 1857 the famous multituberculate genus *Plagiaulax*, which Owen followed up in 1860 with *Triconodon* and in 1866 with *Stylodon*.

It is chiefly the description of the Beckles Collection which fills Owen's renowned "Monograph of the Fossil Mammalia of the Mesozoic Formations" (1871). In this work, which occupies a quarto volume of over 115 pages, with four plates, Owen describes and figures almost every specimen of the Mesozoic Mammalia then known. Written in his clear and interesting style, it is one of the most valuable of that prolific author's many memoirs and is the classic foundation of this branch of palaeontology.

In 1858 Charles Moore had found in a Rhaetic fissure-filling at Holwell, Frome, Somersetshire, a number of teeth closely similar to those found by Plieninger in the Rhaetic of Germany. These teeth were submitted in that year to Owen, who referred them to *Microlestes*, and later, in the monograph of 1871, named them *Microlestes moorei*. In the meantime (1864) Boyd Dawkins, working in the Rhaetic of Watchet, Somersetshire, discovered and described as *Hypsiprymnopsis rhaeticus* a single worn and somewhat problematical tooth pertaining to the same group.

But two years after Dawkins' discovery, and five before the appearance of the monograph, another was added to the list of known Rhaetic forms by O. Fraas (1866), who described as *Triglyphus* a single tooth with a number of cusps arranged in three longitudinal rows.

The date 1871 to which the eventful unfolding of Mesozoic mammalian history has now been followed marks an important turning point. From that time to the present hardly more than half a dozen new specimens have been reported from European strata. Few new names have been added to the lists and only one horizon, the Wealden. The general stagnation of so promising a subject has been remarkable. On the other hand, American palaeontology was then just entering that golden era which followed the opening of the great western fossil fields.

Most of the known American Mesozoic mammals were found by parties collecting for Professor O. C. Marsh, and the largest collection of them is in the Peabody Museum of Yale University, although a relatively large number is in the United States National Museum and there is also some excellent material in the American Museum of Natural History. Two principal American horizons have been productive of Mesozoic mammals, the Morrison and the Lance, the former uppermost Jurassic, the latter uppermost Cretaceous. Both Jurassic and Cretaceous mammals were published by Marsh, but unfortunately only in a very cursory, preliminary fashion, and Osborn also published a general review of the Cretaceous fauna. All the known specimens have recently been studied or restudied by the present writer.

The year 1888 is notable for the appearance of the second comprehensive memoir on the Mesozoic Mammalia, that by Osborn "On the Structure and Classification of the Mesozoic Mammalia." This work fills eighty quarto pages, with two plates of restorations of English forms. It was the first general review relating the many new forms discovered after Owen's work to the classical series described by the latter in 1871, and it included the first attempt to place all the Mesozoic mammals in a natural zoological classification. It was based on a review of the British Museum specimens, including a large part of those used by Owen, on a thorough knowledge of later mammals, and on the published work of Professor Marsh. A few errors

of fact were corrected in the same year after a second visit to England and examination of specimens not seen previously.

In 1881 E. W. Willett described a triconodont mandible from the Purbeckian. Just ten years after this (1891) A. Smith Woodward published the discovery by Charles Dawson of a mammalian tooth in the Wealden of Hastings, and in 1893 Lydekker recorded a similar discovery. In 1911 Woodward recorded the third and last Wealden find, this time by P. Teilhard de Chardin, working under Dawson's guidance. These Wealden specimens remain the only known Lower Cretaceous mammals. Woodward has also described a triconodont maxilla from the Purbeckian (1912). Of other European (or African) work in the present century, but few contributions are to be signalized. One, by Branca (1915), considers in detail all the known Triassic forms, including *Tritylodon*, while another, by Hennig (1922), considers the Rhaeto-Liassic forms of Württemberg and describes several new forms found in the collections. Petronievics (1917, 1918, 1922) has published short notes on *Tritylodon* and on *Stereognathus*, and von Huene (1926) has described a very mutilated but interesting tooth from East Africa. Broom (1905, 1910, 1914) has added greatly to our knowledge of *Tritylodon* and other multituberculates.

The importance of the study of the Mesozoic mammals has been greatly enhanced by the fact that they have come to occupy a central place in theories of cusp evolution, especially in the arguments of the American school. Osborn's "Evolution of Mammalian Molar Teeth" (1907) contains the essence of his deductions as to their importance for this subject, also a new classification which serves as a point of departure for later ones. J. W. Gidley (1906) published excellent figures of a few of the teeth in the United States National Museum, and based on them a criticism of some phases of the Cope-Osborn theory. W. K. Gregory has, in recent years (1910, 1922), given lucid critical reviews of the Mesozoic mammals and their meaning, basing himself largely on the literature of the subject.

One of the most important of recent discoveries is that of the wonderful series of skulls brought back by the American Museum Central Asiatic Expedition from the Cretaceous (Djadochta) of Mongolia. No fewer than seven partial skulls were found by the expedition, yielding information of the most valuable sort, especially as previous to this time only one fragmentary Mesozoic mammal skull had been described (*Tritylodon*).

More than a century has thus elapsed since the first Mesozoic mammal was made known. In that time, which includes almost the entire history of the science of vertebrate palaeontology, most students of fossil mammals have been concerned in some way with the group, from Cuvier to our own contemporaries. Yet the known mammalian faunas stand out like lights in the vast darkness of the Age of Reptiles—and very dim lights most of them are. This mammalian prehistory is two to four times as long as the "historical period" which followed it, and yet the materials for the latter are literally many thousand-fold those for the former. This, however, only makes close scrutiny of the Mesozoic mammals which are known the more necessary, and the results which are to be obtained from them the more precious.

MAMMAL-BEARING MESOZOIC AND PALAEOCENE FORMATIONS.

Age.				Europe.	Africa.	North America.	South America.	Asia.
Palaeocene			Landenian	Cernaysian (France)		Tiffany—Clark Fork—Paskapoo Torrejon—Fort Union Puerco		Gashato
Cretaceous		Upper	Danian			Lance—Hell Creek Edmonton Belly River	"*Proteodidelphys* Beds"	
			Senonian Turonian Cenomanian					Djadochta
		Lower	Albian Aptian Barremian Neocomian	Wealden (England)				
Jurassic	Oolitic	Upper	Purbeckian	Purbeck (England)	Tendaguru	Morrison		
			Portlandian Kimmeridgian Corallian Oxfordian Callovian					
		Middle	Bathonian Bajocian Aalenian	Stonesfield (England)				
	Liassic	Lower	Toarcian Pliensbachian Sinemurian Hettangian					
Triassic			Rhaetic	Rhät-Lias Bone-bed (Germany) Westbury Beds (England) Sully Beds (England)	Stormberg			
			Keuper Conchylian Bunter					

MORPHOLOGY AND TAXONOMY

ORDER MULTITUBERCULATA Cope.

DIAGNOSIS.—Mammalia with upper incisors three, the first much reduced or lost, the second enlarged. One enlarged lower incisor. No canines. Molars with five or more cusps arranged in two or three parallel longitudinal rows. Nasals large, expanding posteriorly. Zygomata arising opposite middle or anterior cheek teeth, widely expanded, and running back almost to occiput. Mandible powerful, with small, low coronoid and no angular process, but with a well-marked pterygoid crest. (Mandible unknown in first suborder.)

DISCUSSION.—This great Order has a recorded history the duration of which is rivalled only by those of the Marsupialia Polyprotodontia and of the Insectivora, and equalled by none. Its members are the Mesozoic mammals *par excellence;* first appearing in the Upper Triassic, they do not vanish until the very end of the Paleocene. Their duration as an Order was longer than that of the deinosaurs and much longer than the entire Cainozoic. They are known from Asia, Europe, Africa, and North America, and occur at every Mesozoic horizon from which mammals are known, save two (from each of which but a single mammalian specimen has been secured).

Owen's memoir of 1871 did not recognize the multituberculates as a natural group, "*Microlestes*" [*Thomasia*] and *Plagiaulax* being widely separated and *Stereognathus* and *Bolodon* placed as *incertae sedis,* but in a later paper (Owen, 1885) he recognized the resemblances of *Plagiaulax, Neoplagiaulax, Tritylodon,* and "*Microlestes*" [*Thomasia*]. Marsh was the first definitely to associate the multituberculates then known into a single Order, which he defined under the name Allotheria (Marsh, 1880) and which he ultimately came to consider as having marsupial affinities (Marsh, 1887).

The term Multituberculata by which the Order is now generally known was first used by Cope (1884) for a Suborder of the Marsupialia, including the families Tritylodontidae, Polymastodontidae, and Plagiaulacidae. A phylogenetic tree was given in which *Tritylodon* gave rise to three branches, one leading to *Polymastodon,* one to all the other later multituberculates and eventually also the Pleistocene marsupial *Thylacoleo,* and one to the Pleistocene and Recent wombat, *Phascolomys.* In 1887 Cope erected the new family Chirogidae, supposed to link the Plagiaulacidae and Polymastodontidae, but since shown to be based on the upper dentition of *Ptilodus.*

Osborn's memoir of 1888 accepted the Multituberculata as a Suborder of

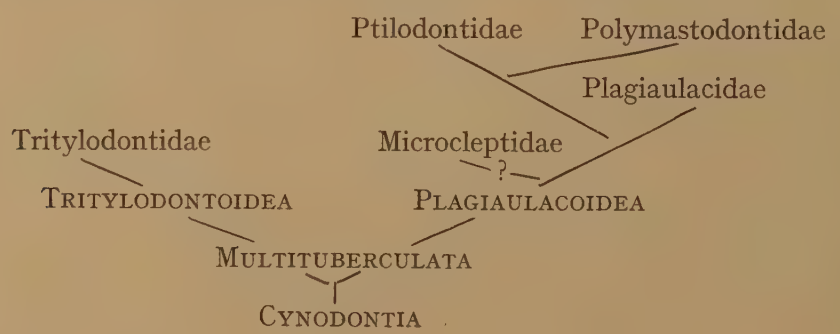
marsupials and included the families Plagiaulacidae, Bolodontidae, Tritylodontidae, and Polymastodontidae, while *Stereognathus* was left as *incertae sedis*. Marsh proposed several new families for the Lance Multituberculates (Cimolodontidae, Dipriodontidae, Tripriodontidae, Cimolomidae—Marsh, 1889) but Osborn later showed (1894) that the members of all these families properly belonged to the Plagiaulacidae, as then understood, while in the following year Osborn & Earle (1895) reduced the family Polymastodontidae to the rank of a subfamily of the Plagiaulacidae. Gidley's paper on *Ptilodus* (1909) clearly showed that the supposed families Allodontidae, Bolodontidae, and Chirogidae were based on plagiaulacoid upper teeth while the corresponding lower jaws had been referred to other families.

There has thus been achieved a two- or three-fold division of the Order into the families Tritylodontidae, Plagiaulacidae, and usually also Polymastodontidae; and this obtains in most recent classifications, although some writers (as Hennig, 1922, and Zittel, Broili, Schlosser, 1923) would include also the South American Polydolopidae of Ameghino. Of these latter forms it must suffice to say here that as complete a study as can be made outside of South America and careful comparisons with all known undoubted multituberculates, firmly convince me that they are neither multituberculates nor relatives of that group.

In the following pages the other three families of recent classifications are all recognized, and evidence is adduced to show that *Thomasia* (*Microlestes*) and *Microcleptes* gen. nov. differ much more from *Plagiaulax* than has been supposed and should be referred to the new family Microcleptidae, of rather uncertain affinities. *Ptilodus* and its allies also are found to show such significant differences from the true plagiaulacids that their reference to the Plagiaulacidae is no longer convenient, and for them the family Ptilodontidae has been proposed (see below, p. 52).

Examining these five families, it is found that one of them, the Tritylodontidae, is very different from the others, certainly was not ancestral to them despite its early appearance, and may even be of distinct ordinal relationships. This great contrast is best expressed at present by the erection of two Suborders, Tritylodontoidea and Ptilodontoidea. The right of the group as a whole to rank as an Order is discussed later, in the section on affinities of the various Orders.

The apparent relationships of the recognized taxonomic units of the Order Multituberculata may be graphically shown in the following way:



Suborder *TRITYLODONTOIDEA*, Nov.

Diagnosis.—Multituberculata having upper molars quadrate, with three rows of two to four cusps each. Cheek teeth little differentiated, at least five molariform teeth of identical pattern, no trenchant pre-molars. Lachrymals and frontals large. Long narrow palate without vacuities and with choanae far forward.

Family TRITYLODONTIDAE Cope.

With the characters of the Suborder.

Tritylodon itself is the only member of this family of which our knowledge, although still slight, is yet adequate for some decision as to relationships. The affinities of the family are therefore those of *Tritylodon*, discussed below, and the other genera are placed here simply on the basis of their resemblance to the type genus.

Genus TRITYLODON Owen.

1866. *Triglyphus* O. Fraas, "Vor der Sündflut," p. 215; *non* H. Loew, 1840, "Posener Zweiflügler," p. 30.

1884. *Tritylodon* Owen, *Quart. J. Geol. Soc., London*, XL, p. 146.

Diagnosis.—Tritylodontidae having upper molars with two outer, four median, and three inner cusps. All cusps save the antero-external, crescentic; but those of external and internal rows, asymmetrical. Anterior root of zygoma opposite second and third cheek teeth.

Genotype.—*Tritylodon longaevus*.

Tritylodon longaevus Owen.

(Pl. I, figs. 1–3; Pl. II, fig. 1; Text-figs. 1–2.)

1884. *Tritylodon longaevus* Owen, *Quart. J. Geol. Soc., London*, XL, p. 146.
See also Seeley, 1895A; Broom, 1905, 1910, 1914; Petronievics, 1917, 1922.

Diagnosis.—Upper molar about 75 per cent. larger than that of the only other known species. Length M^4 7·0 mm.

Horizon and Locality.—Stormberg (Rhaetic) member of Karroo Series, Thaba N'chou, Basutoland, South Africa.

Material in British Museum:

M 1951. Holotype and only specimen. Anterior part of skull. (*By Exchange with Bloemfontein Museum*, 1884.)

Skull.

The form of the part of the skull preserved is well shown in the accompanying illustrations (Fig. 1) as also in those previously published. The narrow interorbital constriction localized the break that caused the loss of the cranium proper. Anterior

to the orbits the face is again somewhat constricted laterally, and then expands slightly to form the blunt and somewhat bulbous snout.

The premaxilla is a small element, consisting of little more than the bony socket into which is inserted the great I^2. Its boundaries (save possibly that on the palate) are so clear that its nature is beyond doubt. Its total length at the alveolar level is about 18 mm., and it ends just behind I^3. Anteriorly, the two premaxillae meet and rise to form a small knob, which has been considered as a rudimentary internarial process. The vertical plates of the premaxillae pass up laterally on each side of the nares, from which, however, they are separated by the septomaxillae, and each ends in a sharp, posteriorly directed point, without reaching the nasals. About 16 mm. of the anterior part of the palate is formed by the premaxillae. A slight ridge or saddle runs transversely between the posterior ends of the second incisors, and the surface anterior to this is concave and rises slightly to the first incisive alveoli. The anterior palatine foramina are relatively small and are just internal and posterior to the third incisors. There also appear to be two small vascular foramina farther forward between the second incisors.

The septomaxillae are very clearly shown. They are prominent on the anterior dorsal surface, extending back some 15 mm. to a sharp point between the maxillae and the nasals. Each passes down as a vertical plate of bone on the admedian side of the premaxilla. Having reached the floor of the nares, these bony plates turn at right angles and pass toward each other at the mid-line, but the ossified portion ceases before this point is reached. Connecting their ends with the nasal septum, however, are the remains of what was evidently cartilage. The nasal septum itself seems to be preserved as a gray granular substance, harder than ordinary matrix but not bony—no doubt also formerly cartilage. These relationships are shown in Figure 1, C, D.

The only serious question as to the nasals which has been or can be raised concerns the posterior suture. One view, that of Broom, makes these bones long and widely expanded posteriorly. The other, older view, recently reaffirmed by Petronievics, makes the nasals much shorter and considers Broom's posterior nasal expansions to be the frontals and Broom's frontals to be the parietals (Owen, Petronievics) or the postfrontals (Seeley). After long study under the binocular microscope, with due attention to the grain of the bone—here clearly displayed—as well as to all other pertinent features, it can only be concluded that the supposed fronto-nasal suture of most students is entirely due to post-mortem crushing and that the sutures as determined by Broom are the correct ones in this respect. Similar long nasals, expanded posteriorly, are found in cynodonts and in many primitive mammals, including the later multituberculates.

This decision as to the nasals involves the determination of the most posterior of the preserved dorsal skull-elements as the frontals. They are represented only by their anterior portions, which are very strong and massive, their surfaces steeply sloping to the great sagittal crest, which begins at their anterior end. This crest is seen in section at the posterior end of the specimen and is made of very solid bone, but the two sides are not, as Owen thought, ankylosed.

The opening or pit between the frontals anteriorly was interpreted by Owen as a fontanelle, or a pineal foramen, or due to posthumous injury. Osborn at first hailed it as a pineal foramen, but later retracted this opinion. Petronievics had this part developed still farther, but without finding any clear evidence of a parietal foramen, although noting that this still seemed possible to him. On the interpretation accepted in this work, this obviously could not be a pineal foramen, as it is at the posterior end of the nasals. At any rate, it has not the aspect of a true pineal foramen,

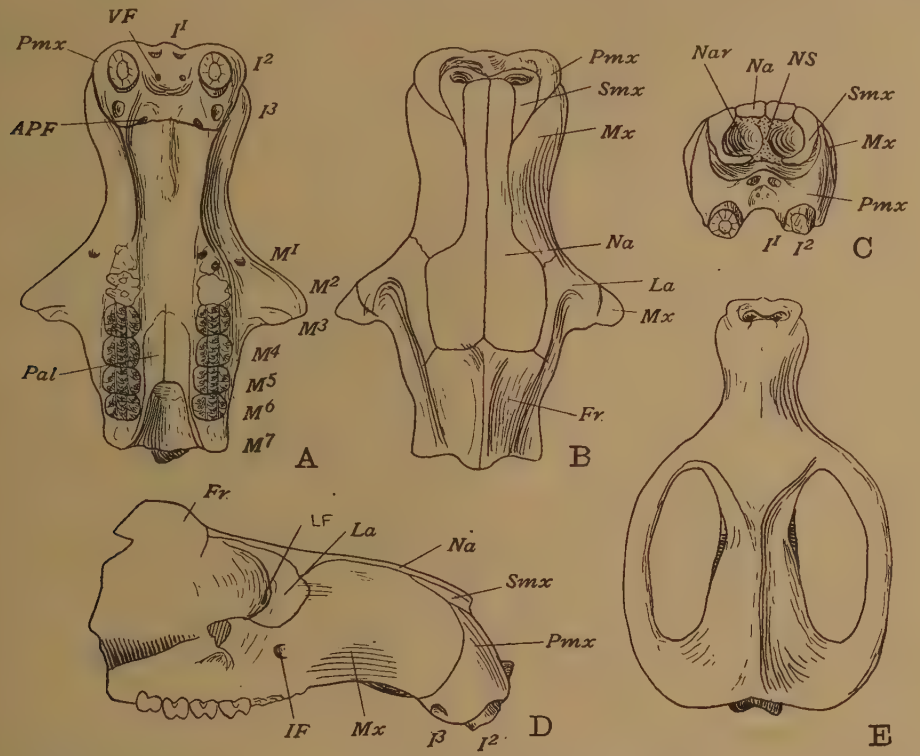


FIG. 1.—*Tritylodon longaevus* Owen. A, palatal view. B, dorsal view. C, anterior view of snout. D, right lateral view. E, hypothetical reconstruction of dorsal view of entire skull. *APF*, anterior palatal foramen. *Fr*, frontal. *IF*, infraorbital foramen. *La*, lachrymal. *LF*, lachrymal foramen. *Mx*, maxilla. *Na*, nasal. *Nar*, anterior nares. *NS*, nasal septum. *Pal*, palatine. *Pmx*, premaxilla. *Smx*, septomaxilla. *VF*, vascular foramen. A–D drawn from the holotype, the two sides being used to complete one another but no hypothetical elements introduced. A–D, × ⅔ diam. E, × ⅓ diam. Rhaetic, Stormberg beds, Thaba-N'chou, Basutoland.

and, as suggested by Owen, it seems undoubtedly due to posthumous causes, probably aided by the fact that ossification was not yet complete here, for the individual was not fully adult.

The bone bounding the anterior part of the superior border of the orbit was interpreted by Owen as the lateral part of the frontal, by Seeley and Petronievics as the prefrontal, and by Broom as the superior portion of a large lachrymal. It cannot be denied that this supposed element is separated from the undoubted lachrymal on each side by a crack, which may or may not follow a true suture. The

latter appears, on the whole, to be the case, and in any event, without denying the possibility, we must demand better evidence than this before accepting the presence in *Tritylodon* of a bone otherwise not represented in the Class to which it belongs.

Even aside from this doubtful part, the lachrymal has a considerable facial expansion. The foramen is well seen on both sides and is within the rim of the orbit. Broom shows one suture within the orbit and Petronievics shows several, but none of these seem at all definite.

The maxilla is a large element forming the greater part of the palate as also of the facial part of the skull. Anteriorly it meets the premaxillae and septomaxillae; superiorly it is separated from its fellow on the other side by the nasals, here narrow; and posteriorly it meets the lachrymal above. The rather small infraorbital foramen is seen just anterior to the lower part of the root of the zygoma. Earlier students have agreed in seeing the anterior end of the jugal in the preserved part of the root of the zygoma. Careful comparison of the two sides under the microscope, however, reveals nothing that can justly be called a suture in this region. On the contrary, it seems possible to assert the continuity of the supposed jugal with the maxilla in places. It therefore appears that there is a strong zygomatic process of the maxilla, and that the jugal was confined to the zygoma and is not preserved.

The maxillary portion of the palate has no vacuities and appears to have no foramina. It is similar to that of *Diademodon*, ending, like the latter, anterior to the end of the cheek teeth, opposite M^5 in this case. Again, as in the cynodonts, the palate involves the palatines posteriorly in spite of its incomplete nature. Behind the palate the palatine forms a thin vertical plate of bone, closely applied to the inner surface of the alveolar process of the maxilla. In its upward course this plate passes between the maxilla and vomer and then into the wall of the orbit. This gives the posterior part of the maxilla an isolated character which has caused it to be misinterpreted when found alone, as in *Stereognathus*, an ally of *Tritylodon*.

Dentition.

Incisors.—The incisors are three in number, the first and third small and represented only by empty alveoli, placed as shown in Figure 1, A. I^2 is represented on each side only by its root, large, oval, undivided, extending well back into the maxillae, as in rodents.

Cheek Teeth.—I^3 is followed by a diastema of some 23 mm., the canine being absent. The cheek teeth, all of which will be called molars for convenience of reference, are seven in number. The first is missing, even to the roots. On the right side there is only a rugose appearance of the alveolar border without any true alveoli. On the left there is a similar rugose appearance, but there are also two pits which seem to be alveoli, one antero-internal to the other.

M^2 is represented on the right side by its roots, and on the left side both M^2 and M^3 are in this conditiou. Left M^4 has the badly battered mid-row of cusps preserved, while M^5 has at present only the anterior cusps of the middle and outer

rows. M^{6-7} have been entirely removed on this side by the preparation executed for Dr. Petronievics (1922).

Right M^3 has the battered mid-row and the posterior cusps of the inner row, which agree closely with those of M^4. The latter is at present the best preserved of all the teeth. The crown is divided into three distinct rows of cusps by two deep longitudinal grooves. These grooves and cusps show signs of considerable wear from the opposing teeth, and the cusps are also damaged by chipping and cracks. The cusp formula (outer-middle-inner rows) is 2–4–3. All the cusps except the antero-external are crescentic, with the crescents opening forwards (as in all selenodont multituberculate upper molars). The cusps of the middle row are symmetrically crescentic, those of the other rows quite asymmetrically so, as shown in the figure. The outer

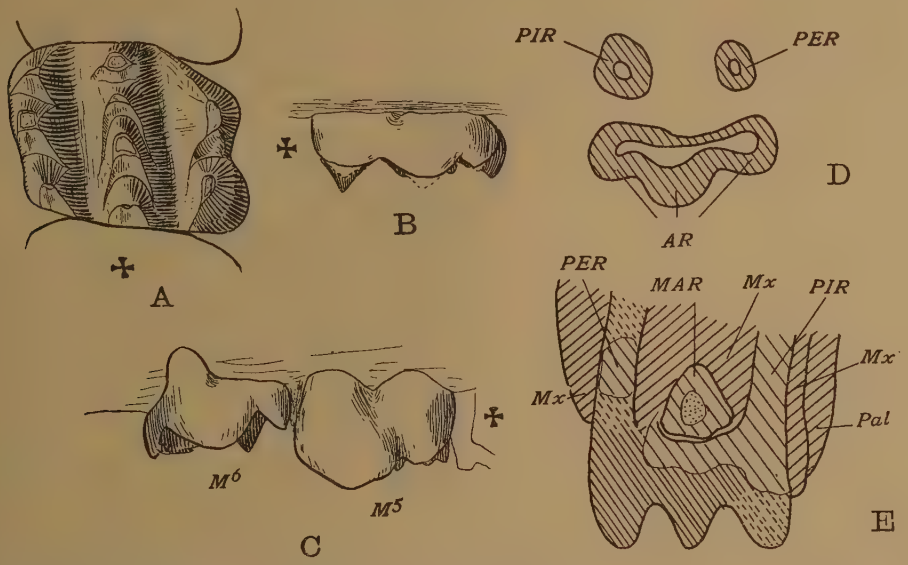


FIG. 2.—*Tritylodon longaevus* Owen. A, crown view of right M^4. B, internal view of same. C, external view of right M^{5-6}. D, horizontal section of the roots of right M^2. E, vertical transverse section through the posterior part of left M^5. *AR*, anterior root. *MAR*, median portion of the anterior root of the following tooth. *Mx*, maxilla. *Pal*, palatine. *PER*, postero-external root. *PIR*, postero-internal root. All drawn from the holotype; × 4 diam.

row is shorter than the other two and has only two cusps, the anterior smaller and lower than the posterior. This anterior cusp is not truly crescentic and sends from its apex but a single crest running to the edge of the tooth at the anterior end of the outer groove. The postero-external cusp is the largest on the tooth and is crescentic, but has the crest which runs into the groove more developed than the other.

The inner row consists of three cusps, the anterior two about the same size, the posterior one smaller. The antero-median cusp is but little worn and is sharp and piercing. It is crescentic and is enveloped laterally by the wings of the succeeding cusp. This latter is the largest of the four cusps of the median row, the next, third, being a little smaller. The fourth is less prominently crescentic and did not envelop the preceding cusp laterally.

Two misapprehensions may here be noticed. The first is that the teeth have been said to be unworn. They are, in truth, very much worn, and the facets and longitudinal striations on the sides of the grooves show abundant evidence of propalinal mastication. The second misapprehension, which has been universal, even among students of the original, is that the cusps have been supposed to be radially furrowed. The cusps have radiating cracks, due to posthumous drying, which simulate furrows or rugosities to the naked eye; but under the binocular microscope, with proper lighting, the enamel is seen to be nearly smooth, with no true surface-sculpturing corresponding to the quite adventitious cracks.

Right M^5 is rather less well preserved and the postero-median cusp is quite gone, but it agrees well with M^4 and supplements the latter in some particulars.

M^6 was described by Owen as rather different in detail from the preceding teeth, but the real differences prove to be due to two causes only: the tooth is a little smaller, and it is less fully protruded from the alveolus. The antero-lateral cusps are still unworn. The two more posterior internal cusps are broken, but their separate bases can be made out. The entire antero-median cusp is broken away, but its former attachment to the crown is well shown. The second median cusp is well preserved save for the loss of enamel from the anterior part of the tip. The third and fourth are represented only by their confluent bases, so that, alone, they would give the impression of a single broken cusp, but comparison with preceding teeth shows that they were quite distinct. The pattern is thus exactly that described for M^4.

Broom suggested that the space behind M^6 might have held another molar, but Petronievics refused to accept this because "the limit of the last molar on the right side is a sharp one, and no plain trace of a molar behind it is to be seen." Not merely a plain trace, however, but the molar itself is still there. It is still within the formative capsule, as should have been suspected from the fact (hitherto overlooked) that the preceding tooth is just coming into use. Nothing of the detailed morphology of this buried germ of M^7 can be made out, but its presence is amply substantiated by the visible enamel of one of the cusps of the mid-row.

Dental Formula.—Owen considered the dental formula to be I^2 C^0 M^6. Broom advanced the formula I^3 C^0 P^4 M^3, while Petronievics prefers I^3 C^0 P^1 M^5. The presence of three incisors and seven cheek teeth and the absence of the canine are open to no question, but the division of the cheek teeth into premolars and molars is quite unsettled. This may be accomplished only by the following methods:

1. By determination of replacement, either by direct observation or by study of the degree of protrusion and of wear of the various teeth. Direct observation is inapplicable and degree of protrusion and wear are about the same on M^{2-5}, while M^{6-7} were progressively later in coming into use, as they would be in any event. This most positive and only really determinative class of criteria is therefore of no use in the present case.

2. By morphological differences. This is the basis of Petronievics' formula, and it is the only one really sanctioned by the material (that is, in the form P^1 M^6); but in view of the extraordinary nature of this formula and of the fact that we really

know nothing whatever of the morphology of the first cheek tooth, the evidence seems inconclusive. M^{2-6}, at least, show no appreciable morphological differences.

3. By analogy with other forms. This is the basis for Broom's formula, but it appears unjustified. The following pertinent facts should be borne in mind: (*a*) *Tritylodon* lived millions of years earlier than the first mammals with an established formula of P^4M^3; (*b*) it was certainly not ancestral to those mammals and its relationship to them is extremely remote, nor is its dentition primitive; (*c*) even those earlier Mesozoic mammals which are clearly nearest to the marsupial-placental line did not have a typical formula of P^4 M^3, while the known multituberculates never even approximated to this formula; (*d*) the formula does violence to the morphology of *Tritylodon*, for it separates teeth which are exactly alike in size, in pattern, in wear, and in degree of protrusion, calling one a premolar and one a molar.

It must be concluded that a satisfactory division of the cheek teeth of *Tritylodon* is not now possible. This conclusion seems a barren one, but the absence of a natural division is a positive and important morphological feature, while it is much better to dispense with a division altogether than to adopt an erroneous one. The formula may be written I^3 C^0 $P+M^7$.

Molar Roots.—Petronievics has put beyond doubt the presence of root division in *Tritylodon*. Incontrovertible as are his main conclusions, some of the details of his descriptions call for slight correction. In Fig. 2, E, is given a new illustration of the preparation made for Dr. Petronievics by slicing down very close to the posterior end of the left M^5. As shown by him, there are distinct cylindrical postero-external and postero-internal roots (our *PER* and *PIR*, his γ and α). There is also a median root (our *MAR'*, his β), but, as shown in Petronievics' sketch (which is accurate though wrongly interpreted in his text), this does not really belong to the tooth in question. It belongs rather to the succeeding tooth, the now missing M^6, which, as shown on the other side of the jaw, was not fully erupted and was crowded up very closely against M^5, while the presence of an antero-median root but of no postero-median one seems to have been characteristic of all the molars. The fact that the pulp cavity, as seen, is closed is simply due to the fact that this is a slicé of the wall of a bulbous swelling.

The true arrangement of the roots may be made out on left M^{2-3} but better on right M^2, of which a section just below the crown is illustrated (Fig. 2, D). The two posterior roots are relatively slender and perfectly distinct, while the anterior half of the crown bears at this level but a single transverse root divided into three swellings, which probably become distinct roots at a point farther from the crown. The median one is the largest, and projects a little in front of the anterior edge of the extra-alveolar part of the tooth.

Affinities.

Previous Views.—Owen (1884) confidently placed *Tritylodon* among the Mammalia. Seeley at first (1888) concurred, calling it a "bunotheroid rodent," but he later (1895) averred that it was not a mammal at all, giving many reasons for this view, but admitting the possibility (later inferentially denied) that it might be in a

sense intermediate between mammals and reptiles. Broom (1905) showed conclusively that Seeley's arguments against mammalian affinities were invalid and that *Tritylodon* must have had a squamoso-dentary articulation and hence must have been a mammal. In 1910 Broom again emphasized these points, and showed *Tritylodon* to be even less reptile-like than he had previously believed. More recently (1917) Petronievics has reverted in large part to earlier conceptions of the cranial osteology, but without denying its mammalian nature, for proof of which he especially relies on the root division as demonstrated by him.

As to its position in the class, advocates of the mammalian nature of *Tritylodon* have all referred it to the Allotheria or Multituberculata. In 1884 (immediately after its description) Cope established for it the family Tritylodontidae, defined by having the "fourth superior premolar (at least) like true molars." In this family he included *Stereognathus*. Osborn in 1888 placed *Tritylodon* and *Triglyphus* in this family, with *Stereognathus* as *incertae sedis*, and gave the family a new but indecisive definition. He later placed *Stereognathus* in a new family, along with some Upper Cretaceous forms, but he abandoned this family in 1894. In 1910 he was content to call *Tritylodon* simply a multituberculate *incertae sedis*. Most recent writers refer *Tritylodon* to the Tritylodontidae, a family of multituberculates co-ordinate with the one, two, or three later families recognized.

Tabulation of Characters.—The simplest way to sum up the evidence as it now appears is in tabular form :

A. Definitely non-mammalian characters shared with the Cynodonts :

None.

B. Characters shared with the cynodonts but also seen in some primitive mammals :

1. Presence and structure of the secondary palate.
2. General form of facial part of skull.
3. Relatively large ossified septomaxillae.
4. Size and shape of nasals.
5. Character of lachrymals.

C. Mammalian characters not shared with cynodonts (see also under D).

1. Wear of teeth, implying a direct squamoso-dentary articulation.
2. Divided molar roots.
3. No postorbital bar.
4. No postorbital or postfrontal bones.
5. Apparently no prefrontal bone.
6. No complete internarial process.
7. Typical mammalian infra-orbital and lachrymal foramina.

The characters listed under these three categories, especially when those listed under D are added, are conclusive as regards the mammalian affinities of *Tritylodon*. It shows no diagnostic reptilian characters, but has all the diagnostic mammalian features which could be shown by the parts preserved. Indeed, as Broom was the first to point out, the character numbered C 1 is in itself conclusive. This, with all

the other evidence, is so strong that it is impossible not to consider *Tritylodon* as a true mammal.

D. Multituberculate characters (also adding to the evidence against reference to the cynodonts).

1. Dental formula $I^3\ C^0\ P+M^7$ as in plagiaulacids.
2. I^2 much enlarged and rodent-like.
3. Molars with many cusps arranged in parallel rows.
4. Zygomata arising opposite cheek teeth.
5. Maxillae with strong zygomatic processes.
6. General habitus herbivorous, rodent-like ; mastication propalinal.

These facts are so striking that *Tritylodon* has generally been referred to the Multituberculata without especial discussion. This is unfortunate, in a way, for it has caused most students to overlook the fact that *Tritylodon* is clearly and deeply differentiated from the typical multituberculates. It is not too much to say that there is more difference between the dentition of *Tritylodon* and that of the typical multituberculates closest to it in point of time—plagiaulacids—than there is between the teeth of a horse and those of an opossum.

E. Characters distinguishing *Tritylodon* from later multituberculates, save *Stereognathus :*

1. At least five molariform cheek teeth of identical pattern.
2. No shearing teeth.
3. Upper molars quadrate, with two to four cusps in each of three rows.
4. Most of the cusps strongly crescentic.
5. Lachrymals and frontals large.
6. Septomaxillae prominent.
7. Bulbous expansion of snout.
8. Long narrow palate without vacuities and with choanae far forward.

Of the total known significant characters of *Tritylodon* those in which it differs from the other multituberculates form an unexpectedly large percentage. 1 and 2 are especially striking : later forms not only never have more than two molariform teeth, and these usually far from identical in pattern, but even when the posterior upper premolars come superficially to resemble the molars, they are yet clearly seen to be derived from simpler, less molar-like forms. The shearing teeth, so typical of all later forms, except when lost secondarily (*Polymastodon*), are not present in *Tritylodon ;* indeed, the corresponding teeth are the most molariform of any, they cannot have been derived from shearing teeth nor, with due regard to the morphology of the latter, can they have given rise to them.

3 and 4 are very striking differences from the Upper Jurassic forms, in which the cusps are yet truly crescentic and the upper molars are elongate, with only two rows. The Upper Cretaceous and Paleocene forms, however, are rather like *Tritylodon* in these respects, although the very different proportions, cusp formulae, and details of cusp shape make the resemblance a superficial one. The Ptilodontidae do have

three rows of crescentic cusps in the upper molars, as does *Tritylodon*, but it can be shown beyond reasonable doubt that the ptilodontid condition was derived from that of the plagiaulacids or of forms very like them, by the addition of cusps to the ends of the rows, by the upgrowth of a new cusp row (still incomplete in most) and by the development in each cusp of a rather complicated crescentic or quadrate ridge pattern. Ptilodontids being derived from plagiaulacids, and plagiaulacids being much later than and quite different from *Tritylodon*, it follows that such resemblance as does exist between the ptilodontids and *Tritylodon* must be due to convergence or parallelism. How far this may be trusted as an index of *ordinal* relationships depends on how firmly one may believe in the tendency, call it homoplasy or what you will, for forms of similar ancestry to achieve similar final morphological types independently. To see an example of this tendency in two groups separated by such a truly vast stretch of time—all of the Jurassic and most of the Cretaceous—is a demand on faith rather more severe than any which this conception has elsewhere demanded of its adherents.

In any event, the details of the dentition in the three groups, tritylodontids, plagiaulacids, and the direct or collateral descendants of the latter—ptilodontids and polymastodontids—show very conclusively that *Tritylodon* was not ancestral to any of the latter, that, if related at all, its relationship was that of a remote and independent phylum of the same order, and that the only really striking points of resemblance are manifestly secondary and due to convergence.

The characters listed under 5 and 6 are primitive, but have a certain bearing on the problem, as the loss or reduction of the lachrymal was already well established in the plagiaulacids, while the later forms, and perhaps also the plagiaulacids, differ conspicuously from *Tritylodon* in the absence of septomaxillae and lachrymals and in the great reduction of the frontals.

7 is an adaptive character of doubtful phylogenetic bearing, although fitting in well enough with the other evidence. 8 may also be primitive, but in view of the characteristic and quite constant development of the palate in other forms, considerable significance cannot be denied to it.

Conclusions.—The morphological facts and their interpretation as set forth above, involve the following conclusions as to the affinities of *Tritylodon*:

1. It is a mammal.
2. It is probably, but by no means surely, a member of the Order Multituberculata.
3. Within this Order it is so peculiar, so clearly cut off from almost all of the other forms, that it must be placed in a distinct Suborder, as defined above.

Tritylodon fraasi Lydekker.

(Text-fig. 3.)

1866. *Triglyphus* gen. caelebs, O. Fraas, "Vor der Sündflut," p. 215.
1887. *Tritylodon fraasi* Lydekker, Cat. Foss. Mamm. B. M. (N. H.), V, p. 201.
1922. *Triglyphus fraasi* Hennig, *N. Jahrb. Min. Geol. Paläont., Beil. Bd.*, XLVI, p. 241.
See also Neumayr, 1884, p. 279; Osborn, 1888A, p. 220; Branca, 1915, p. 19.

DIAGNOSIS.—Upper molars markedly smaller than those of *Tritylodon longaevus*.
HORIZON AND LOCALITY.—Rhaetic of Schlösslesmühle, Württemberg.
MATERIAL.—None. The type and only specimen has been lost.

This tooth, an isolated molar found in 1860, was first described by O. Fraas in his "Vor der Sündflut" (1866) with figures from every aspect. The original has been lost and we are confined to old figures and descriptions which are inadequate to present conceptions and which do not inspire entire confidence in their detailed accuracy. Neumayr (1884) pointed out that this tooth resembled that of *Tritylodon*. Lydekker (1887) considered the two congeneric and called the German form *Tritylodon fraasi*. The so-called "*Triglyphus*" and a molar of *Tritylodon* are identical in shape and in number and arrangement of cusps, and they are of nearly or quite the same age. Hennig (1922) suggests three differences as validating generic separation: the presence of radial grooves on the cusps of *Tritylodon*, the larger size of the latter, and the conical rather than crescentic cusps of the German form. The first has been shown in the preceding pages to be erroneous; the second is at best a specific and not a generic character; while one is permitted to believe that the third is erroneous as regards "*Triglyphus*." All other three-rowed multituberculate teeth of whatever age have crescentic cusps, and this detail could easily be overlooked in such a small and probably worn tooth, especially when viewed with the imperfect optical instruments of the day.

FIG. 3.—*Tritylodon fraasi* Lydekker. Holotype upper molar from various aspects, from Lydekker after Fraas. Central figures nat. size, others × 2 diam. Rhaeto-Lias, Württemberg.

In the absence of other evidence one can only conclude that this lost tooth must be referred to *Tritylodon*. The earlier name *Triglyphus* cannot be applied to the genus, as it was preoccupied by a genus of Diptera, and in any event has no scientific standing as against *Tritylodon*, since it was not associated with a specific name until after the latter had been properly defined.

GENUS CHALEPOTHERIUM nov.

DIAGNOSIS.—Based on a single broken molar with tall, upstanding, well-separated cusps, some, at least, crescentic. In one row, probably the middle, there are three cusps; a lateral row was shorter, with but two cusps.

GENOTYPE.—"*Microlestes*" *plieningeri* Ameghino (1903, p. 165).

DISCUSSION.—This new genus is formed for the reception of the larger specimen referred to "*Microlestes*" by Plieninger. The specimen was named *M. plieningeri* by Ameghino. The holotype is so broken that it would have been preferable to leave it unnamed. Since, however, this is not the case, and since the species does not appear to belong to any established genus, least of all to *Thomasia* (=*Microlestes*), it is necessary to give it a new generic name.

The generic name is from the Greek χαλεπός, vexatious, and θηρίον, wild beast.

Chalepotherium plieningeri Ameghino.

1903. *Microlestes plieningeri* Ameghino, *An. Mus. Nac. Buenos Aires* (3), II, p. 165.

DIAGNOSIS.—The only species of the genus.

HORIZON AND LOCALITY.—Uppermost Rhaetic, or lowest Lias of Württemburg; probably from the Schlösslesmühle, near Steinenbronn.

MATERIAL.—The only specimen is in the Naturaliensammlung, Stuttgart.

Single broken molar. Figured Plieninger, 1847, fig. 4; Lyell, 1855, fig. 442; Falconer, 1857, fig. 17; Ameghino, 1903, p. 165.

DESCRIPTION.—After the figure of Falconer, 1857, this specimen seems to have been neglected, and the original was not again studied until 1927. In 1921 Hennig stated that the original was either lost or damaged beyond recognition, but in this he was mistaken.

There are two rows of cusps. One row has three distinct cusps, of which two are crescentic, and one is smaller and partly embraced by the wings of the following crescent. There was another straight cusp-row, separated from the first by a deep, straight groove, but this is now broken off. If one may rely on the old figures, it was composed of two cusps. A third row may have been present, but no evidence for or against this is now available. There are at least two stout roots.

AFFINITIES.—Although referred at first to *Microlestes*, i.e. *Thomasia*, this tooth has obviously nothing to do with that genus. It clearly belongs to the larger tritylodontid group, with its well separated, straight rows of crescentic cusps. It thus invites comparison with *Tritylodon* and *Oligokyphus*, and may possibly belong to one of these genera, although it presents clear differences from the teeth so far known. The presence of two cusps in one row and of four in another is sufficient to distinguish *Chalepotherium* from all other Rhaetic mammals.

GENUS STEREOGNATHUS Charlesworth.

1854. *Stereognathus* Charlesworth, *Rept. Brit. Ass.*, p. 80.

DIAGNOSIS.—Tritylodontidae having upper molars with two outer, two median, and two inner cusps. External and internal cusps not crescentic, with but one crest from apex. Anterior root of zygoma apparently anterior to cheek teeth.

Stereognathus ooliticus Charlesworth.

(Text-figs. 4, 5, 6.)

1854. *Stereognathus ooliticus* Charlesworth, *Rept. Brit. Ass.*, p. 80.

See also Owen, 1857, p. 1; 1861, p. 345; 1871, p. 18; Marsh, 1887, p. 343; 1891, p. 613; Osborn, 1888A, p. 221; Goodrich, 1894, p. 424; Petronievics, 1918, p. 67.

DIAGNOSIS.—The only species of the genus.

FORMATION AND LOCALITY.—Stonesfield Slate at Stonesfield, Oxfordshire.

MATERIAL.—*a*. In the British Museum:

M 4000. Cast of holotype.

b. In Museum of Practical Geology, London : Holotype, part of the right maxilla with three broken molars and alveoli for three more. Figd., Owen, 1857, Pl. i, and 1871, Pl. i, figs. 27–30 ; Phillips, 1871, fig. 83 ; Petronievics, 1918, Pl. iii.

c. In the University Museum, Oxford :

Part of a left maxilla with roots of four molars, one of which has the postero-internal cusp preserved. This specimen was found about 1861 by a schoolfellow of E. Ray Lankester, the latter recording its discovery in *The Geologist* of that year (p. 310) in a letter erroneously ascribed to E. Ray of Lanbeater. It was taken to Huxley, who cleaned the cusps of the molars, but later it was very badly damaged. Huxley put the specimen away and subsequent search failed to uncover it. Its existence is mentioned in Goodrich, 1894 (p. 18), but it had not then been found. It was, however, rediscovered very soon after, and placed in the University Museum at Oxford, where it has since remained. It has never been figured or adequately described.

The following discussion is based on the actual holotype, unless the contrary is specifically stated.

Dentition.

Molar Crowns.—The first alveoli preserved are distinctly narrower, especially anteriorly, than those which follow, so that this tooth was probably near the beginning of the series, perhaps M^1 or M^2.

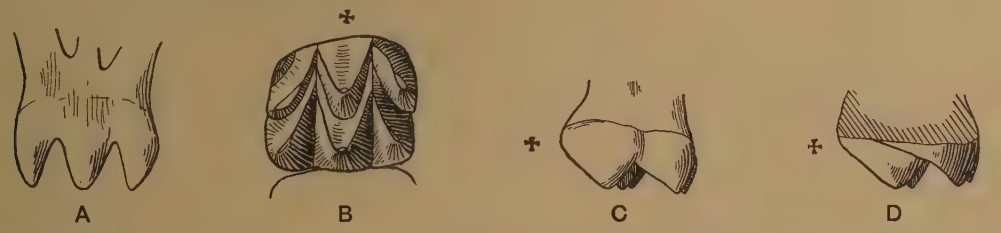


Fig. 4.—*Stereognathus ooliticus* Charlesworth. Right upper molar, reconstructed from the several molars of the holotype. A, posterior view. B, crown view. C, internal view. D, internal view with the internal cusp-row removed. The cross marks the anterior end. All × 6 diam. Middle Jurassic, Stonesfield Slate, Stonesfield, Oxfordshire.

The first preserved molar, by this count M^4 or M^5, retains the central cusps, in a rather worn condition, but the lateral ones are quite broken away. The next molar is the most complete, but the postero-external cusp is missing as are also the posterior ends of the postero-median and postero-internal cusps, giving them a singular aspect not original to them. The cusp formula is 2–2–2 on this tooth, without any observed tendency toward the addition of other cusps. The cusps of the external and internal rows are placed *en échelon*, the posterior cusp sending from its apex but one crest which passes mediad of the anterior cusp. The anterior cusp also sends a single ridge from its apex, passing forward and somewhat medial, roughly parallel to the other crest. Between the lateral rows and the median one are deep longitudinal grooves.

The median cusps are crescentic, compressed transversely, with two slightly diverging crests passing forward from each apex, and the crests of the posterior cusp embracing the base of the anterior cusp. The anterior faces of the cusps between the crests are plane or slightly concave.

The grooves are parallel to each other and to the longitudinal axis of the jaw, but the cusps are not exactly arranged in transverse lines at right angles to this. If a line be passed through each median cusp normal to the longitudinal axis of the jaw, the corresponding internal cusp will be somewhat anterior to the line, the external one somewhat posterior to it.

The surfaces of the teeth are rather worn and chipped. Each groove shows wear from an opposing row of lower cusps, while the median cusp row is worn and rounded from wear in the median groove of the lower teeth. The lateral cusp rows, on the contrary, seem to be worn only on the slope towards the groove, indicating that the lower teeth had but two cusp rows.

The last of the preserved teeth has lost both outer cusps, but it has retained the somewhat worn and battered median and inner ones. No definite differences from the corresponding parts of the preceding tooth can be seen.

FIG. 5.—*Stereognathus ooliticus* Charlesworth. External view of the Oxford specimen. × 4 diam. Middle Jurassic, Stonesfield Slate, Stonesfield, Oxfordshire.

MOLAR ROOTS.—The anterior three sets of alveoli have been exposed at different levels from the alveolar mouths, due to the breaking away of part of the bone. The anterior set presents the deepest section. At this level there are five roots: one small median longitudinal, and two outer and two inner. Just before the roots join the base of the crown there is seen but one long outer and one similar inner root, the two occurring in each case at the deeper level having united. It was this fact that led Petronievics into the error of supposing there to be but three roots.

The teeth are quite high-crowned, even the highest root division taking place farther from the wearing surface than in *Tritylodon*, for instance.

OXFORD SPECIMEN.—The exposed side of this specimen is apparently external, but the original surface is worn away, exposing part of the molar roots. Two roots are visible externally, a larger postero-external and a smaller, more median, antero-external. There is also a separate postero-internal root and probably the same number occurred as in the other specimen. The only cusp preserved agrees with a corresponding one of the type. It is almost unworn and the specimen must have been an unusually good one before it was accidentally damaged.

MAXILLA.

The only part of the jaw preserved consists of a bony process just large enough to accommodate the roots of the molars borne by it. The alveolar border is nearly straight, while the suborbital border is slightly arched, so that the body of the bone

is deeper at the two ends than in the middle. The earlier belief that one end of the jaw is markedly deeper than the other seems to have been due to a failure to recognize that part of the alveolar border is broken away at the supposed anterior end.

On the surface, which all agree to be external, the bone is smooth and glistening, save for one series of slight longitudinal striations where it turns from vertical to horizontal. It is slightly swollen near the teeth, but soon curves inward, the section being very nearly that of an arc of a circle of small radius. On the inside the bone passes straight away from the alveoli and is not smooth, but rather rough, with numerous shallow longitudinal grooves or large striations. The one signalized by Petronievics as the mylohyoid groove is simply one of these markings, more marked than the rest, and has not the character of a true internal groove as seen in the

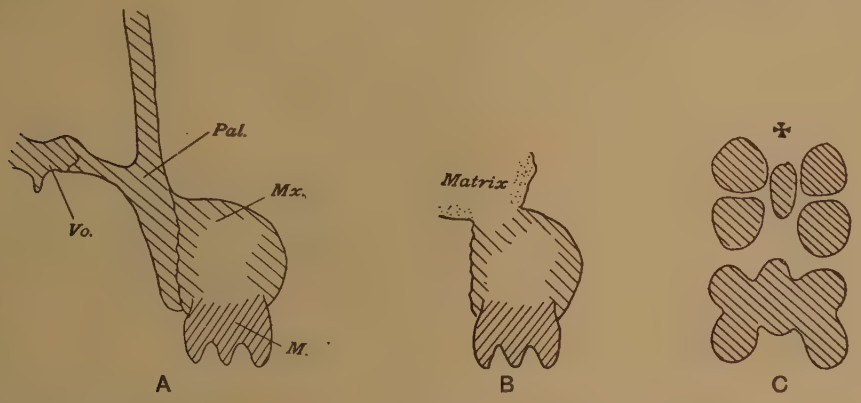


FIG. 6.—*Stereognathus ooliticus* Charlesworth. A, diagram showing in vertical transverse section the probable relationships of the posterior part of the maxilla. B, diagram of the vertical transverse section of the holotype as preserved. C, horizontal sections of the roots of two molars, the anterior one cut at a deeper level. *M*, molar. *Mx*, maxilla. *Pal*, palatine. *Vo*, vomer. A–B, not to scale. C, × 6 diam.

lower jaws of many Mesozoic mammals. Furthermore, the internal groove never occurs in multituberculates.

When this jaw was first described by Owen he considered it to be a lower one. Marsh, however, stated that it was the posterior end of a maxilla (1887, p. 343). With a view to settling this question, Petronievics had a little more of the jaw exposed, and concluded that it must be a mandible (1918). Matthew examined the specimen still later (in 1920) and reached the conclusion that it was, indeed, an upper jaw despite its isolated and rather rod-like character. (Opinion expressed in Gregory, 1922, p. xiii, also in personal communication.) D. M. S. Watson examined the jaw at the same time and concurred in this finding. The following considerations seem to show that this view is the correct one :

1. The molars are very close to the upper molars of *Tritylodon* in general character.

2. Molars of this type with three rows of cusps always belong to the upper and never to the lower jaw in analogous and related animals.

3. The supposed internal groove cannot be such.

4. The rough inner face can only be interpreted as a sutural surface for the

palatine. The posterior part of the alveolar process of the maxilla is quite similar in character in *Tritylodon* and offers a satisfactory explanation of the original relationships in *Stereognathus*.

The specimen being, then, an upper jaw, it follows that the root of the zygoma was anterior to at least six of the cheek teeth and hence somewhat farther forward than in *Tritylodon*. The fragment is interpreted as belonging to the right maxilla, because in *Tritylodon* and all other selenodont multituberculates the crescents of the upper molars open forwards, and for this to be the case also in *Stereognathus* the specimen would have to be from the right side.

Affinities.

The only known mammal which approaches at all closely to *Stereognathus* in character is *Tritylodon*. The two agree in the following important features:

1. Presence of six or more similar cheek teeth.
2. Upper molars quadrate, with three rows of crescentic or crested cusps. Cusps relatively few in number.
3. Similar character and relationships of posterior end of maxilla.

These are the most essential of the known features of *Stereognathus* and, at least in the present very imperfect state of our knowledge of that form, leave us no choice but to refer it to the Tritylodontidae. The following are the more important differences from *Tritylodon*:

1. Cusp formula 2–2–2 rather than 2–4–3, and lateral cusps somewhat different in shape.
2. Size smaller.
3. Root of zygoma farther forward.

These differences are generic but not, as they stand, of greater value.

Measurements.

Lengths of molars: Anterior	3·1 mm.
Median	3·3 mm.
Posterior	3·2 mm.
Width of median preserved molar	3·6 mm.
Height of alveolar process of maxilla above median molar	4·0 mm.

Genus OLIGOKYPHUS Hennig.

1922. *Oligokyphus* Hennig, *N. Jahrb. Min. Geol. Paläont., Beil. Bd.*, XLVI, p. 206.

Diagnosis.—Tritylodontidae having upper molar with three outer, four median, and three inner cusps. Median cusps crescentic, cusps of other two rows asymmetrically or not crescentic.

Genotype.—*O. triserialis* Hennig.

Hennig based this genus on two teeth which he has figured so well and discussed at such great length that it is fitting here only to give a very brief description for comparative purposes and to point out one or two differences in interpretation. One tooth Hennig considers as an upper molar, the other probably as an upper

premolar, and he places them in different species. This is a legitimate procedure, as their relationship to each other is uncertain, and these species are therefore retained here, although it is very probable that the two teeth represent upper and lower molars of the same or very closely allied species.

Oligokyphus triserialis Hennig, 1922.

(Text-fig. 7.)

1922. *Oligokyphus triserialis* Hennig, *N. Jahrb. Min. Geol. Paläont., Beil. Bd.*, XLVI, p. 206.

DIAGNOSIS.—Length 4 mm. Artificially distinguished from the other species by having three cusp rows.

FORMATION AND LOCALITY.—Rhaeto-Lias Bone Bed, probably either from Olga-Hain or the Schlösslesmühle, Württemberg.

HOLOTYPE.—A single upper molar. Figd., Hennig, 1922, Pl. III, fig. 5.

In Tübingen University Museum.

DESCRIPTION.

This specimen, the origin of which is not very clear, was preserved at Tübingen under a common label with the following one. It was referred to *Triglyphus*, but Hennig very rightly found essential differences from all other mammals and placed the tooth in a new genus.

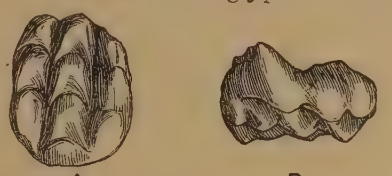


FIG. 7.—*Oligokyphus triserialis* Hennig. Views of the holotype, redrawn after Hennig. A, crown view. B, lateral view. × 5 diam. Rhaet-Lias, Württemberg.

The crown consists of three straight longitudinal rows of cusps. The median row is the longest and begins at one end with a small, short, somewhat transverse cusp. The three succeeding cusps of the same row are of the same size and shape, each being fairly prominent, rather bluntly pointed, narrowly crescentic by reason of two angulations which descend anteriorly from the apex of each and embrace between them the base of the next preceding cusp.

The lateral cusp rows are less clearly formed. One begins anteriorly with a long cusp which sends forward but a single indefinite ridge and hence is not crescentic. It is succeeded by a higher but shorter cusp which is definitely crescentic, but not symmetrically so, the ridge towards the mid-row being more strongly developed. Behind this is another much smaller asymmetrically crescentic cusp. The other lateral row forms, as it were, a longitudinal wall which is not as strongly marked off into separate cusps as are the other two rows, although its crest forms three distinct cusps. This rather indefinite nature is no doubt largely due to wear or post-mortem damage, and at least the middle cusp still shows evidence of having been asymmetrically crescentic.

The roots are broken off, but there appear to have been four of them, one at each angle of the crown.

ORIENTATION.—After several pages of discussion, Hennig reaches no entirely

definite conclusion as to the orientation of the tooth. It seems, however, that this may be established with considerable probability although, of course, not with certainty. In all selenodont multituberculates, including *Tritylodon*, the arms of the crescents of the upper molars point forwards. Moreover, in *Tritylodon* as in *Oligokyphus* the anterior end of the mid-row is marked by a simpler cusp, which is embraced by the wings of that next following. The anterior end of the tooth is thus fixed almost with certainty. As to which side is external, this is much more doubtful (although it is not very important, both the lateral rows having the same cusp number). In *Stereognathus* and, more obscurely, in *Tritylodon* the internal cusps are slightly in advance of the middle ones, the external ones somewhat behind them. If this be true also of *Oligokyphus*, then the tooth must be a left upper molar. This seems very likely for the further reason that it makes the two antero-external cusps closely resemble those of *Tritylodon* and leaves the acquisition of the very small postero-external cusp as the only difference in the external row. That the tooth is an upper and not a lower molar is obvious from the four roots and three cusp rows.

Affinities.

Hennig has also devoted much space to a discussion of the affinities of *Oligokyphus*, and he apparently considers its closest allies to be *Tritylodon* and *Triglyphus* (also = *Tritylodon*)—an unimpeachable conclusion. A quadrate, selenodont tooth with three cusp rows of not more than four cusps each can only be compared with *Tritylodon*. The number, form, and arrangement of the cusps is sufficiently close to leave little doubt that real affinity is indicated. The chief differences, validating generic separation, are as follows :

1. There are three cusps, rather than two, in the outer row.
2. The cusps of the internal row are less distinctly crescentic.
3. The antero-median cusp is somewhat smaller and the succeeding median cusps are more nearly equal in size.

Oligokyphus biserialis Hennig.

(Text-fig. 8.)

1922. *Oligokyphus biserialis* Hennig, *N. Jahrb. Min. Geol. Paläont., Beil. Bd.*, p. 225.

Diagnosis.—Length about 3·5 mm. Artificially distinguished by having two cusp rows.

Formation and Locality.—Rhaeto-Lias Bone Bed. Olga-Hain, near Bebenhausen, Württemberg.

Holotype.—Single lower molar. Figd., Hennig, 1922, Pl. ii, fig. 11.
In Tübingen University Museum.

Description.

This tooth is almost the only one from the German Rhaeto-Lias that has an authentic and complete history : it was found in 1901 by Schmierer at the place

indicated, and was preserved in the collection of the Geologisches-Paläontologisches Institut of the University of Tübingen under the name *Microlestes* until Hennig, in 1922, referred it to *Oligokyphus* and arbitrarily placed it in a new species for convenience of reference.

The tooth is elongated and has but two rows of three cusps each. The stoutest cusps of each row stand opposite each other at the anterior end. One row is slightly weaker than the other; its second cusp is distinctly smaller than the one opposite it, and its posterior cusp, while longer than its mate, is thin transversely and rather wall-like, at least in its present condition. The two anterior cusps of each row are crescentic. The enamel is smooth, and the crown is implanted by two roots of which the posterior one is stouter.

Orientation.—Hennig reaches the conclusion that this tooth is an upper premolar, probably from the left side, but it seems almost certain that it is a lower molar. On the assumption that the higher end is anterior, as it very probably is, Hennig thinks that the tooth must be an upper tooth for the crescents to point in the right direction; but in this he is mistaken, for this would make the wings of the crescents point backwards, which they never do in the upper jaw. The tooth must be a molar, for multituberculate premolars never have crescentic cusps and are never adapted to antero-posterior grinding—the only possible exception is *Tritylodon;* but it does not cloud the issue, for in it all the upper cheek teeth have three rows and cannot be surely divided into molars and premolars. The tooth is in all probability a lower molar, for the following reasons:

Fig. 8.—*Oligokyphus biserialis* Hennig. Views of the holotype, redrawn after Hennig. A, lateral. B, posterior. C, crown. D, inferior. × 5 diam. Rhaet-Lias, Württemberg.

1. No selenodont multituberculate upper molar with only two cusp rows is known.

2. If, as all agree, the high end is probably anterior, then the crescents would point in the usual multituberculate direction only if the tooth is a lower.

3. The only other selenodont multituberculates of anything like comparable antiquity, *Tritylodon, Oligokyphus, Stereognathus,* are known only from upper molars, but in each case the upper molars have three rows of cusps from the arrangement and wear of which it is clear that the opposing teeth had but two rows.

As to which side is external and which internal, there is no adequate basis for a conclusion. The sides are very nearly alike and this does not greatly matter.

Affinities.

This tooth was long accepted (although not published) as *Plieningeria antiqua.* Hennig is obviously correct, however, in separating it from that genus very sharply. It is not a microcleptid and resembles that group only in a most superficial fashion. Its six subequal cusps arranged in perfectly parallel rows and its selenodont character exclude it from the Microcleptidae and allow comparison only with the Tritylodontidae and Ptilodontidae. The same reasons which lead one to believe that the resemblance

of *Tritylodon* to the ptilodontids is secondary and convergent also apply here. Furthermore, the cusp pattern is not really that of the ptilodontids, despite the fact that both are selenodont in a broad sense of the term. The real resemblance is clearly with the tritylodontids. According to our knowledge of the upper molars of this group, we should necessarily infer lower molars with two rows of two to three cusps each, at least the more anterior cusps definitely crescentic, the lower molars in any individual being distinctly narrower and slightly shorter than the upper molars. The holotype of *Oligokyphus biserialis* fits these conditions exactly, indeed it would serve admirably for a lower molar of *Oligokyphus triserialis*, the difference in dimensions being what would be expected, although the present tooth is a little too narrow to belong to the same individual as the genoholotype. Both may very likely be from the same locality—Olga-Hain. *O. biserialis* is the only known tritylodontid lower tooth, unless *Archaeodon reuningi* is also one.

? Tritylodontoidea Incertae Sedis.

Several other teeth have been found in the Rhaeto-Lias of Württemberg and considered to be related to *Tritylodon* or to *Plieningeria*. None of them have any great scientific value at the present time, but they may be briefly mentioned.

1. A specimen in the Stuttgart Cabinet once believed to be a forgery (see below). Hennig discusses this tooth at some length (1922, p. 234 *seq.*) and points out that it is not a forgery, but that it is by no means certain that it is a mammal tooth. It is an irregularly broken nodule, but with the remains of three cusp-like swellings on one side. Re-examination shows that it certainly is not mammalian.

2. Wetzel's specimen from Bebenhausen. This was also described by Hennig (1922, p. 238) and is triangular with three indefinite swellings, two of them united to the third by two ridges. This is not certainly a mammal tooth.

3. Several specimens at Tübingen, one of which may be mammalian and resembles the above two. Described in Hennig, 1922, p. 239. For teeth of the type of these last three Hennig proposes the name *Stathmodon*—but the name is not validated by the application of a specific name, and it does not seem worth while to take that step. The specimens are so very problematical as to be of slight significance.

4. Forgeries. The supply of Triassic mammal teeth unfortunately does not equal the demand and enterprising manufacturers have undertaken to remedy this situation. Osborn (1888A, p. 221, fig. 14) figured a specimen from the collection of the Hohenheim Academy in which he placed no great trust but which he thought might be a premolar of a tritylodont, if actually from the Rhaetic beds. Marsh (1891, p. 4) stated very positively that this was a forgery and that he had a similar one in his possession. Unfortunately the figured specimen was lost just after the figure was drawn, but Marsh's specimen is still in existence. Although obviously spurious on detailed study, the naked eye detects the forgery only with greatest difficulty. Hennig (1922, p. 235) mentions another similar imitation in the Heidelberg collection, and there are probably a number of others scattered about.

Suborder *PLAGIAULACOIDEA*, Nov.

Diagnosis.—Multituberculata with molars two in number, the first, at least, elongated and both with two or with three rows of two to twelve cusps each. Premolars sharply differentiated from molars, the posterior ones forming a strong shearing device (secondarily lost in one family). The lachrymal reduced or absent, the jugal and frontal much reduced, with progressive overlapping of the latter by the parietal. Zygomatic process of the maxilla strong, with a squamosal contact. Palate usually broad, extending back as far as end of tooth series, and with vacuities.

Discussion.—To this Suborder should be referred the families Plagiaulacidae, Ptilodontidae, Polymastodontidae, and, rather doubtfully, also the Microcleptidae. The typical family, that of the Plagiaulacidae, is well represented in the Purbeck fauna. The ptilodontids are represented in Europe only by the Cernaysian forms, but they are generally taken as being of post-Mesozoic age and are excluded from the present monograph, although the family is defined. The Polymastodontidae are exclusively American, so far as known, while the Microcleptids are European, being recorded from England and Germany.

In dealing with plagiaulacoids it is slowly becoming possible to gain some idea of the direction in which they evolved, from Jurassic to the end of Paleocene times. In the case of the Tritylodontoidea nothing of the sort can be done, for, so far as the extremely scanty materials go, this type appears fully formed and does not advance significantly. Plagiaulacoids, on the other hand, are known from several horizons, and appear to show marked and fairly evolutionary progress. Although the plagiaulacids were perhaps not directly ancestral to the later forms, yet it is reasonable to assume (on evidence to be more fully detailed later) that they fairly represent the Upper Jurassic stage of development of this group, and if our phylogenetic conclusions are valid, then a comparison of the Plagiaulacidae, Ptilodontidae, and Polymastodontidae will give a fair conception of plagiaulacoid evolution. The chief trends so far observed are as follows :

1. The second upper incisors become relatively larger in *Polymastodon*, with restriction of the enamel areas. The third incisor becomes smaller and less important. In *Djadochtatherium* (from the Middle Cretaceous of Mongolia) it becomes curiously specialized (Simpson, 1925). In the other forms, so far as definitely known, no remarkable changes occur in the upper incisors.

2. The lower incisors tend to become scalpriform with restricted enamel band. This tendency is fully exemplified in but one ptilodontid, *Eucosmodon*, but it is at a high point in the Polymastodontidae.

3. The upper premolars tend to become restricted in number, while those that remain often increase the number of cusps. The upper shearing teeth, two in one phylum and one in another, tend to lose the outer cusps—a specialization which has occurred three times, independently : in *Psalodon* among plagiaulacids, and in *Cimolodon* and *Ectypodus* among ptilodontids. In the polymastodontid line the shearing function is lost, and the premolars are reduced to one above and one below.

4. The number of lower premolars tends to regular reduction, the last one becoming relatively larger and, at least in the smaller forms, acquiring a higher number of grooves with the passage of time. In polymastodontids, however, this tooth is reduced and changed in form.

5. The molars become relatively larger, the first more so than the second, so that although subequal in the Jurassic they are very unequal in all later forms. The number of cusps of at least the first molar increases very considerably, and in both upper molars a supplementary row of cusps grows up progressively. The cusp form becomes ridged and crescentic or quadrate.

6. So far as can be judged, the smaller forms did not change much in general skull characters, but some forms, especially *Polymastodon*, became much larger, with more massive skull and more powerful jaws.

Family PLAGIAULACIDAE Gill.

Diagnosis.—Plagiaulacoids with premolars five above and four or three below, the lower ones shearing against the subequal last two upper ones. Molars upper and lower all of about the same size, with only two rows of cusps in each and not over four cusps in any one row. Molar cusps not definitely crested or truly crescentic.

Discussion.—To this family are referred at present the genera *Plagiaulax*, *Bolodon*, *Ctenacodon*, *Psalodon*, and *Loxaulax*. *Loxaulax* is known only from isolated molars, while *Bolodon* includes upper dentitions of the English forms. As regards the lower jaws, *Ctenacodon* is definitely the most primitive genus and has four lower premolars. *Plagiaulax* shows slight advances—the loss of one premolar, rather more massive jaw, and greater development of grooves on premolars—and there is little doubt that a form very like *Ctenacodon* was ancestral to *Plagiaulax*. The American *Psalodon* has advanced considerably beyond *Ctenacodon* in the upper jaws, if those of the latter are correctly identified, although the lower jaw may not have been very different.

In the Wealden *Loxaulax* is seen a form a little younger than any of the others and very badly known, but so like *Ctenacodon* that one need not hesitate to include it provisionally in this family. Cusp form and differentiation have advanced over *Ctenacodon*, but so far as may be judged from isolated molars, it is derivable from this genus.

There are thus at least four distinct genera in the family, with a limited range of variation, forming a compact group. One type, *Ctenacodon*, might well be ancestral, structurally, to the others. The origin of the family is not certainly found in any earlier known mammals, although it has been suggested that the Rhaetic microlestids are related.

Genus PLAGIAULAX Falconer.

1857. *Plagiaulax* Falconer, *Quart. J. Geol. Soc. London*, XIII, p. 261.

Diagnosis.—Plagiaulacidae with three lower premolars, P_2 very small, not serrated, not shearing, buttress-like against P_3. Ridges on shearing teeth not

confined to edge but extending far down on to face. Jaw becoming shorter and stouter than in *Ctenacodon*.

GENOTYPE.—*P. becklesii* Falconer.

Plagiaulax becklesii Falconer.

(Pl. II, figs. 5–6 ; Pl. III, figs. 1–2 ; Text-fig. 9.)

1857. *Plagiaulax becklesii* Falconer, *Quart. J. Geol. Soc.*, London, XIII, p. 262 ; Owen, "Foss. Mam. Mesozoic," 1871, p. 77.

1871. *Plagiaulax medius* Owen, "Foss. Mam. Mesozoic," p. 85.

See also Lydekker, 1887, pp. 197–8 ; Osborn, 1888A, p. 215.

DIAGNOSIS.—The only known species of this genus.

FORMATION AND LOCALITY.—Middle Purbeckian of Durdlestone Bay, Swanage, Dorset.

MATERIAL.—All the known specimens are in the British Museum, and all in the Beckles Colln., purchased 1876.

47731. Holotype. Right mandibular ramus, the anterior portion with the incisor and three premolars seen in outer aspect on one slab, the posterior portion with the molar alveoli and coronoid and condylar processes seen in internal aspect on the counterpart. Figd., Falconer, 1857, figs. 1–5 ; Owen, 1871, pl. iv, fig. 10.

47728. Left mandibular ramus, outer aspect, with the incisor and all the premolars preserved. Holotype of *Plagiaulax medius* Owen. Figd., Falconer, 1857, fig. 14 ; Owen, 1871, pl. iv., figs. 7 and 12.

47732. Part of right ramus, free of matrix, with base of incisor, the first two premolars, and the anterior half of the third. Figd., Falconer, 1857, figs. 11–13 ; Owen, 1871, pl. iv., figs. 13–14.

47733. Fragment of right ramus with the two molars. Figd., Falconer, 1857, figs. 7–10 ; Owen, 1871, pl. iv., fig. 12.

47734. The left incisor and premolars in outer aspect, the mandible being absent. Figd., Owen, 1871, pl. iv., fig. 15.

In establishing the species *P. medius*, which he based on a specimen referred to *Plagiaulax becklesii* by Falconer and not studied by Owen, the latter relied chiefly on the shorter incisor and shorter premolar series, noting that the former might be due to age or sex and that the differences in the mandible might be due to crushing. It is now clear that the smaller mandible and apparently shorter incisor are simply due to the younger age of the specimen, while the other differences are all due to crushing. As regards the size of the premolars, Owen was misled, for they are exactly the same size as in 47731. The two species must be considered synonymous.

DENTITION.

INCISOR.—The incisor is stout, with a long root extending back underneath the premolars. In the normal position of the jaw it extends forward and slightly upward,

the distal portion being somewhat recurved. The apex is pointed, not chisel-like, and the superior face of the distal portion is gently concave and separated from the outer face by a distinct longitudinal angulation. There is a feeble median longitudinal depression on the proximal part of the external face. As seen in 47732, where it is broken off a short distance above the alveolus, the incisor is somewhat irregularly elliptical in section, the long axis parallel with the longitudinal axis of the jaw. So far as can be made out on the available material, the entire extra-alveolar portion of the tooth is enamel-covered. In 47728 the incisor is much shorter than in the other specimens, but this is a juvenile character, the incisor not being fully protruded. It is also apparently more erect in this specimen, in consequence of crushing.

PREMOLARS.—There are only three premolars, which may be designated P_{2-4}, as it is certainly P_1 of the more primitive *Ctenacodon* which is missing. P_2 is much reduced in size and has taken on the character of P_1 in the latter genus. The crown takes no true part in the shearing edge of the other premolars, but rises from a somewhat swollen base to a simply pointed apex. The whole crown fits closely into a groove in the anterior end of P_2 and serves, so to speak, as a strengthening buttress for that tooth. There are two roots, the posterior one smaller than the other.

The last two premolars together form a curved shearing edge, the posterior part of it, the last two-thirds of the edge of P_4, being nearly horizontal, and the anterior part, the front of P_4 and all of P_3, curving rather sharply downward anteriorly. Despite the sharp thin edge to which they rise, the bases of the premolars are quite thick transversely, and the section of each is that of a stout wedge. The shearing edge is serrate, being marked by small saw-tooth-like projections, five on P_3 and eight on P_4. From each of these projections, except the first on the tooth, there runs forward and downward on to the outer face of the tooth a fine, sharp, curving ridge. These ridges are long in this genus, the first four on P_4 running to the anterior edge of the tooth, while the last three run to the base of the crown. These ridges are also well developed on the inner faces of the last two premolars, as seen in 47732.

On P_3 the posterior of the two roots is smaller, and the outer face of the crown is produced inferiorly into a plump, heel-like projection outside the upper part of the root. The external face is rhomboid, the apex, next to P_4, being at one of the acute angles of the rhomb and the basal projection forming the other. P_4 is also implanted by two roots, but here the posterior one is a little stouter than the anterior. The external face is not a vertically elongated rhomb, but is roughly rectangular and slightly longer, horizontally, than it is high. There is an antero-basal swelling here also, but it is very slight.

The most remarkable feature of P_4, however, is its row of tiny basal cusps, not noticed by any previous student of the group although common to all members of the Plagiaulacidae, so far as known. This consists of a number of small, upward-directed projections—six in this case—arranged in a horizontal series along the lower part of the posterior two-thirds of the outer face of the last premolar. These cuspules are best seen in 47728, a young individual in which P_4 was just coming into use, so that they are quite unworn, although some were broken when the specimen was cleaned. Shear against the posterior upper premolars very quickly truncated these

cusps, and it is only in an exceptionally young specimen that they are clearly seen, although their bases may be made out even in adult, but not aged, specimens like 47731. There is no corresponding structure on the inner face of this tooth.

Molars.—The molars are known only from 47733, and as they are not here associated with the premolars, their reference to this species is not proven, although the size and other relationships make it sufficiently probable. These molars are fairly well preserved, but very badly worn. Each clearly has two longitudinal rows of cusps separated by a deep longitudinal median groove. On M_1 there are two outer and three inner cusps. The inner cusps are the least worn and consequently are the highest cusps on the tooth, as it now is, although they may not have been so originally. The anterior cusp, which is preceded both on its external and on its internal face by a slight vertical depression, as if there might have been a vestigial or incipient cusp anterior to it, has a smooth, semi-conical, unworn inner face, but is much worn on its outer face. The postero-internal cusp is, however, worn on both sides and on the apex, and the thick enamel has been worn through, exposing the dentine. The external cusps are so worn that very little enamel remains on them; but the bases of three cusps, of which the posterior is the largest and the anterior the smallest, can be clearly made out.

On M_2 the inner cusps are both worn and broken, and the outer cusps so badly worn as to be quite indistinguishable one from another. It would be utterly rash to attempt to establish the number of cusps on this tooth from this material.

Mandible.

The horizontal ramus is short and stout, being mostly occupied by the large root of the incisor and, above this, the lesser roots of the cheek teeth. The mental foramen is small and is in a median position just behind the opening of the incisive alveolus (as best seen on 47732). Below the cheek teeth is a curved, rounded ridge, which passes backward into the anterior border of the coronoid; and below this ridge is a slight longitudinal concavity. The coronoid process is rather small and feeble in comparison with the very stout horizontal ramus. Its apex appears to have been rounded and slightly recurved.

The corono-condylar notch is pronounced and nearly semicircular. The condyle itself has a slightly constricted neck and a clearly defined, somewhat convex articular surface, the latter being irregularly ovoid, with its long axis in the vertical plane. From its lower end there passes forward along the postero-inferior border of the jaw a pronounced, inward-projecting pterygoid crest, but there is no indication of an angular process. The shallow pterygoid fossa is rather flat and featureless, but ends anteriorly at a well-defined boundary just below the posterior end of M_2. The dental foramen is at the antero-inferior end of this fossa.

In 47728 the mandible is apparently very different in character from that of the other specimens of the species, but apart from a slight difference in size due to the greater youth of this specimen the differences are all due to crushing. The apparent condyle is not such in reality, but merely a broken end of bone an uncertain distance in front of the condyle. The median part of the coronoid process, figured by Falconer

as being then preserved (1857) has since been broken, but its general character is clear and there is no reason to believe in real morphologic distinction from that of 47731.

MEASUREMENTS.

Maximum horizontal lengths in millimetres :

Specimen.	P_{2-4}.	P_2.	P_3.	P_4.	M_1.	M_2.
47731	5·6	0·8	1·5	3·3	—	—
47728	5·6	0·8	1·5	3·3	—	—
47732	—	0·7	1·7	—	—	—
47733	—	—	—	—	1·8	1·85
47734	5·6	0·6	1·7	3·3	—	—

GENUS CTENACODON Marsh.

1857. *Plagiaulax* Falconer (*pars*), *Quart. J. Geol. Soc.*, London, XIII, p. 261.
1879. *Ctenacodon* Marsh, *Amer. J. Sci.*, (3), XVIII, p. 396.
1884. *Plioprion* Cope, *Amer. Nat.*, XVIII, p. 691.

DIAGNOSIS.—Plagiaulacidae with four lower premolars, P_2 shearing, with or without serrations, relatively larger than in *Plagiaulax*. Ridges on shearing teeth confined to region near edge. Jaw longer and more slender than in *Plagiaulax*.

GENOTYPE.—*C. serratus* Marsh.

DISCUSSION.—The genus *Ctenacodon* was founded by Marsh in 1879 and is based on specimens from the Morrison Formation (Upper Jurassic) of Wyoming. Of American species based on lower jaws two are here recognized : *Ctenacodon serratus* Marsh, the genotype, and *C. scindens* (new species, see p. 37). Although full knowledge of the upper dentition might modify this arrangement, it is impossible to separate the English forms described as *Plagiaulax minor* Falconer and *P. falconeri* Owen from this genus, whereas they show very definite distinctions from the genotype of *Plagiaulax*. Cope was the first to recognize the latter fact, in 1884, when he made *P. minor* the type of a new genus, *Plioprion*. Osborn (1888) rejected this genus on the basis that it would also have to include *Plagiaulax medius*, and that that species is very close to the genotype of *Plagiaulax*. The latter statement is certainly true, for we believe the two to be synonymous, but it is not true that the so-called *Plagiaulax medius* would enter into the genus *Plioprion*, and the latter is unquestionably distinct from *Plagiaulax*. Its distinctive features, however, are just those of the previously defined *Ctenacodon* Marsh, of which genus it is thus a synonym.

The chief differences between the four species of this genus may readily be put in tabular form :

	C. serratus. Size taken as 100.	*C. scindens*. Size 112.	*C. minor*. Size 100.	*C. falconeri*. Size 150.
$\frac{\text{Length } P_4}{\text{Length } P_3}$	=1·54.	1·82	2·00	2·20
Projections on shearing edges of P_3 and P_4, 3 and 6, respectively.		3 and 6	4 and 7	4 and 8
P_4 higher relative to length than in other species.		—	—	—
Antero-internal cusp of M_1 small.		A little larger.	Much reduced or absent.	Unknown.

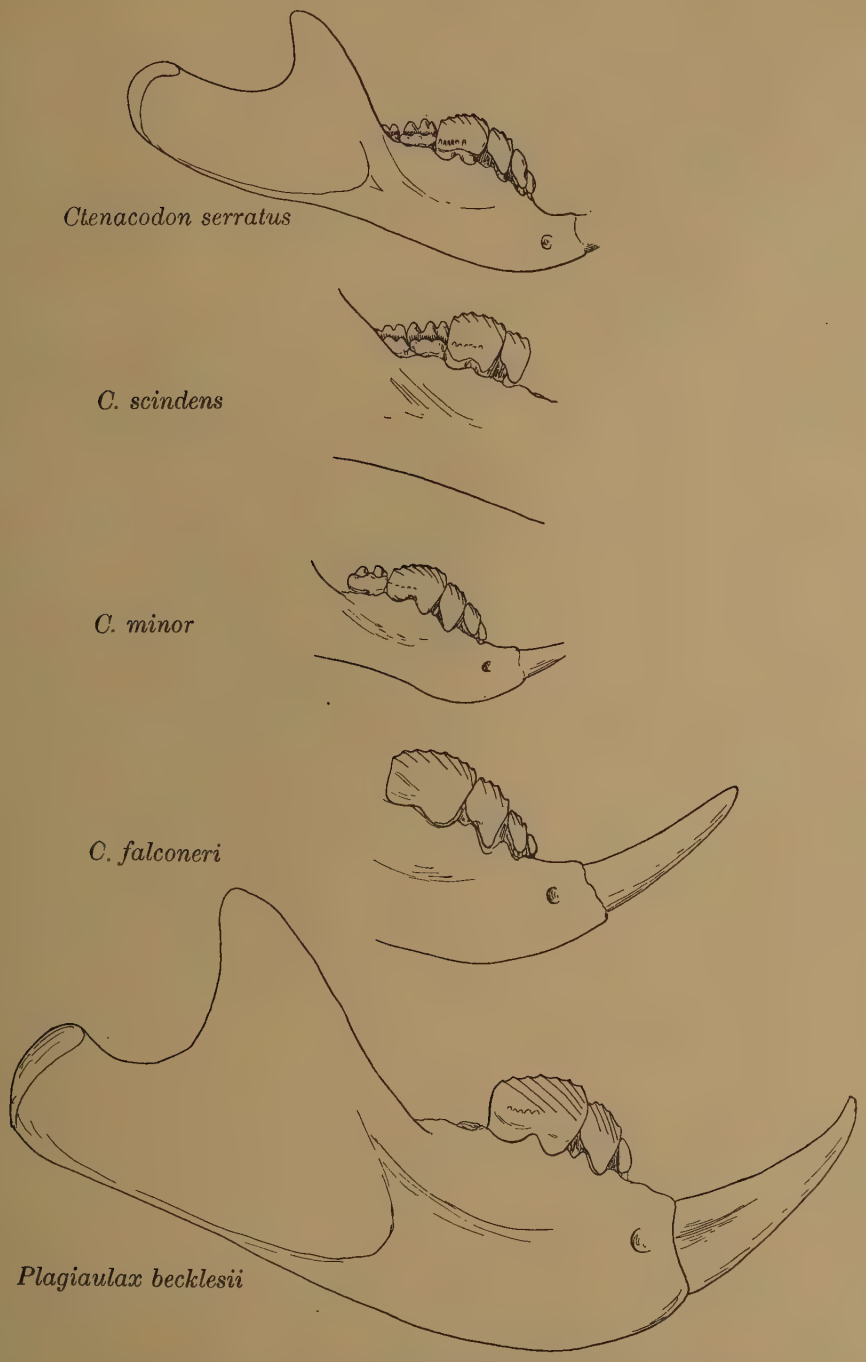


FIG. 9.—Comparative view of the external aspects of the right mandibular rami of the known species of *Ctenacodon* and *Plagiaulax*. All × 4 diam.

The amount of divergence within the genus is seen to be quite small, at least as regards the lower jaws; it would probably be much more noticeable in the upper dentitions, as they show a considerably greater morphological range in the Plagiaulacoidea. The greatest difference in size, between *C. serratus* or *minor* and *C. falconeri*, is only about 50 per cent. of the size of the smaller species. As regards the emphasis placed on the last premolar the various species fall into an interesting graded series. This is apparently a progressive feature, as it tends in the direction of the Cretaceous ptilodontids with their very large P_4 and vestigial P_3.

As would be expected, the two English species resemble each other somewhat more than they do the American forms, and the same is true of the American species with respect to the English ones, but nothing in the known features of the lower jaws permits their separation into two genera. The two English species might be held to be slightly more advanced, but the evidence for this view is not of a very conclusive nature.

Ctenacodon minor Falconer.

(Pl. III, figs. 4–5; Text-fig. 9.)

1857. *Plagiaulax minor* Falconer, *Quart. J. Geol. Soc. London*, XIII, p. 264.

1884. *Plioprion minor* Cope, *Amer. Nat.*, XVIII, p. 691.

See also Owen, 1871, p. 75; Lydekker, 1887, p. 198; Osborn, 1888A, p. 215.

Diagnosis.—Length of premolar series 4·1 mm. in the holotype. P_4 twice as long as P_3. Four projections on shearing edge of P_3 and seven on P_4. Antero-internal cusp of M_1 vestigial.

Formation and Locality.—Purbeckian of Durdlestone Bay, Swansea, Dorset.

Material.—The following specimen, in the British Museum, is the only one certainly referable to this species:

47729. Holotype. Right ramus, external aspect, with most of the incisor and with well-preserved P_{1-4} and M_1. Figd., Falconer, 1857, fig. 15; Owen, 1871, pl. iv., fig. 9; Osborn, 1888, fig. 7 (3, 3*a*). (*Beckles Coll. Purchased* 1876.)

Dentition.

Incisor.—The incisor is a rather smaller and more slender tooth than in *Plagiaulax becklesii* and it has no median external longitudinal depression at the base. The superior posterior portion is devoid of enamel.

Premolars.—The premolars form a wall-like shearing series similar to that already described in *Plagiaulax*, but here P_1 has the small, buttress-like form of P_2 in the more advanced genus, while P_2 has much the same shape as P_3, although smaller and with fewer serrations. The shearing edge of P_2 has three projections and that of P_3 has four. As in *Plagiaulax*, curving ridges run downward and forward from each of these projections except the most anterior, but here these ridges are much shorter relatively than in *Plagiaulax*, being almost wholly marginal in position.

The external faces of both of these teeth are rhombic with an antero-basal expansion or heel-like extension, as already noted for P_3 of *Plagiaulax*. Each is implanted by two roots, of which the anterior is the larger.

P_4 closely resembles the same tooth in *Plagiaulax*. The roots are more nearly equal than in the preceding teeth, the projection downwards outside the anterior one less marked. The shearing edge is more curved, the posterior part being nearly horizontal and the anterior part passing over into that of the preceding tooth at an angle of about 45° to the horizontal. This edge has seven projections and, correspondingly, six slight, sharp ridges run down on to its lateral face. The worn bases, now almost confluent, of a series of nodular projections are to be seen along the posterior two-thirds of the base of the outer face of the crown.

MOLARS.—M_1 is well preserved and only moderately worn. It has five cusps—two inner and three outer. The outer cusps are worn on both sides and on top, the inner only on the side toward the mid-groove. The base of the antero-internal cusp shows a distinct vertical grooving, which passes up anterior to the apex, and this suggests, although it does not prove, that there was here another cusp, as in the American species of the genus, but smaller than in the latter and perhaps also rendered less conspicuous by wear. The outer cusps are exactly like those of *Ctenacodon serratus*, the two posterior ones of nearly equal size, the anterior one smaller and also more worn as it is sometimes reached by the premolar shear.

It is extremely unfortunate that the crown of M_2, which seems at one time to have been present and essentially complete, is now entirely missing, only the roots remaining. As described by Falconer, Owen, and Osborn, the tooth had a broadly basined interior with an elevated rim, the outer part of the rim appearing to bear a number of denticles, the inner part with one prominent anterior cusp, followed by a prolonged ridge not divided into cusps. This concurrence of high authority can leave no question as to the general morphology of the tooth, despite its unfortunate loss, but a great deal of doubt still remains as to the interpretation of these facts. The following considerations seem to lead to a rather different conclusion from that hitherto held:

1. The individual is fully adult and the teeth are much worn, M_2 being, among plagiaulacids, the tooth which receives the most severe usage of all.

2. The broadly basined nature of the crown, as figured and described, clearly indicates advanced wear.

3. Except for this tooth, the jaw agrees in all essential features with those of the American species of *Ctenacodon*, but in the latter M_2 is positively known to have had a simple pattern of six cusps in two rows of three each. It seems extremely improbable that the English form would agree so well in other respects and differ so violently in this one point.

4. In some worn American specimens of *Ctenacodon*, however, an apparently multicuspidate outer row is developed by the wearing through of the enamel, and it seems at least possible that this had happened in *C. minor*, making it seem that there were many small cusps in the outer row whereas there may have been originally but three.

5. These considerations are further strengthened by the improbability that M_2 would differ so much from M_1. While not identical, these two teeth are at least built on the same plan in all other Jurassic multituberculate jaws, upper or lower, in which the facts are known.

While it is necessary to recognize that only a reasonable probability can be established, in the absence of the original tooth, yet it seems a just conclusion that the apparently unique form of M_2 of this specimen was simply due to wear, and that originally it was a simple tooth with five or six cusps arranged in two parallel rows. At least, this appears to be the hypothesis upon which we must proceed until more material is secured.

Mandible.

Only that part of the mandible is preserved which holds the roots of the teeth. This is not very characteristic, but agrees well with the corresponding part of the American species of *Ctenacodon* and also agrees generally with that of *Plagiaulax* save for being more slender and elongated.

Ctenacodon ? minor Falconer.

Material.—The following specimen is in the British Museum, and is from the same horizon and locality as the above:

48399. A crushed fragment of the right jaw, seen in internal aspect, with the four premolars. Associated under the same number are a left fourth premolar, apparently not of the same individual, the broken root of an indeterminate tooth, and an indeterminate fragment of the jaw with no teeth preserved. (*Beckles Coll. Purchased* 1876.)

This material has never been figured and is incorrectly described in Lydekker (1887, p. 199). The teeth of the main fragment are quite unworn and beautifully shown. The enamel surface is very delicately rugose, the rugosities tending to follow the same direction as the marginal ridge on the inner face of the tooth. The unworn nature of the teeth leaves no doubt whatever that the limitation of these ridges to the strictly marginal region is a real difference from *Plagiaulax* and not simply due to wear.

The assignment of this jaw to the genus *Ctenacodon*, as now understood, is certain, but its reference to *C. minor* is doubtful. The premolars are 25 per cent. larger than in the type, but agree in all other characters, so that one would not be justified in erecting a new species on this difference of size.

Of the other three fragments associated under this number, only the isolated fourth premolar is of any value. It probably is referable to *C. minor*, although its somewhat smaller size makes it improbable that it is correctly associated with the other fragment under the same number.

Measurements.

Maximum length in millimetres :

Specimen.	P_{1-4}.	P_1.	P_2.	P_3.	P_4.	M_1.	M_2.
47729 (holotype)	4·1	0·3	0·8	1·0	2·0	1·1	ca.1·1
48399	5·2	0·5	1·0	1·25	2·5	—	—

Ctenacodon falconeri Owen.

(Pl. III, fig. 3 ; Text-fig. 9.)

1871. *Plagiaulax falconeri* Owen, " Fos. Mam. Mesozoic," p. 84.

Diagnosis.—Length of P_{2-4} 5·9 mm. in the holotype. P_3 noticeably less than half as long as P_4. Four projections on shearing edge of P_3 and eight on P_4.

Formation and Locality.—Purbeckian of Durdlestone Bay, Swanage, Dorset.

Material.—The following specimen is in the British Museum :

47730. Part of the right mandibular ramus in outer aspect with the incisor, roots of P_1, and crowns of P_{2-4}. Holotype and only known specimen. Figd., Owen 1871, pl. iv, fig. 16. (*Beckles Coll. Purchased* 1876.)

Dentition.

The long slender incisor, tapering to a rather blunt point, is like that of *C. minor*, but larger. It appears to be more erect, but this is because of the way in which the jaw is broken. P_1 is missing, and P_{2-3} differ appreciably from those of *C. minor* only in size. P_3 has a rather different aspect, but this is largely due to the breaking away of part of the antero-inferior portion. P_4 differs from that of *C. minor* in being larger both absolutely and relatively to the other teeth, in having one more projection on its cutting edge, and in the fact that the posterior portion instead of being noticeably less deep than the anterior, as in the smaller species, is sensibly of the same depth. The bases of the horizontal row of cuspules may be faintly seen. A slightly oblique groove has been worn on the posterio-inferior portion of the external face by wear from M^1 as the jaw was drawn backward in mastication. The slight vertical ridge noted by Owen, and supposed to characterize this species and *C. minor* as opposed to *Plagiaulax becklesii*, is due entirely to wear.

Mandible.

The small portion of the mandible preserved agrees in proportions and other characters with that of *C. minor* and differs only in size.

Measurements.

Maximum lengths in millimetres :

	P_{2-4}.	P_1.	P_2.	P_3.	P_4.
47730	5·9	—	1·1	1·5	3·3

Genus BOLODON Owen.

1871. *Bolodon* Owen, "Fos. Mam. Mesozoic," p. 54.

Diagnosis.—An artificial genus for the reception of Purbeckian plagiaulacid upper jaws, probably synonymous in part with *Plagiaulax* or *Ctenacodon* or both, but not yet definitely correlated with the lower jaws. Cheek teeth: P^5 M^2. P^{1-3} triangular, tricuspid. P^{4-5} shearing teeth with two longitudinal series of conical cusps.

Discussion.—This genus was based by Owen on two fragmentary maxillae. He compared them with *Stereognathus* but confessed himself at a loss to correlate them with any known Purbeckian lower jaws. Marsh (1881, 1887) discovered a similar genus in the Morrison of Wyoming, which he named *Allodon*. He referred both *Bolodon* and *Allodon* to the Plagiaulacidae, but in 1889 speaks of "the family named by the writer the Allodontidae"—a family nowhere defined and representing an unfortunate yielding from his earlier correct but unappreciated stand. In his memoir (1888, p. 217) Osborn discussed the possible relationships of *Bolodon* and *Plagiaulax*, but the defects in the knowledge of both upper and lower jaws at that time led him to assign them to different families.

Fig. 10.—Comparative crown views of the known parts of the upper dentitions of the species of *Bolodon*. All × 6 diam. Upper Jurassic, Middle Purbeck Beds, Swanage, Dorsetshire.

This placing of upper and lower dentitions in different families long obtained also for the later, Paleocene, multituberculates, but in 1909 Gidley described a specimen of *Ptilodus* with upper and lower jaws in actual association, proving beyond any further doubt that the supposedly distinct family Bolodontidae, or Allodontidae, or Chirogidae simply represented the upper dentitions of the forms then referred to the family Plagiaulacidae.

Although associated specimens have not yet been obtained from the Jurassic, it will be seen from what follows that the detailed morphology of *Bolodon* shows it certainly to belong to the family *Plagiaulacidae*. It is retained as a distinct name because the lack of association makes it impossible as yet to ascertain which of its species should be placed in *Plagiaulax*, which in *Ctenacodon*, or if there is not, possibly, a valid third genus here.

Three specimens are known which must be referred to this genus. Although two of them were referred to *Bolodon crassidens* by Owen and even combined into a single composite figure by Osborn, it is certain that they belong to three quite distinct species. It is thus necessary to add the two new species *Bolodon osborni* and

B. elongatus. The three species of *Bolodon* may be compared with the best known Morrison upper jaw, now denominated *Ctenacodon laticeps* (Marsh), as follows :

C. laticeps.	*B. crassidens.*	*B. osborni.*	*B. elongatus.*
I^3 very unlike that of *B. crassidens.*	—	Unknown.	Unknown.
P^{1-3} with three cusps, no heels.	Much as in *C. laticeps.*	No heels. P^3 with incipient fourth cusp.	Heels on P^{1-3}.
P^4 with three outer cusps.	Two outer cusps.	Three.	Unknown.
M^1 with four outer cusps.	Unknown.	Three.	Unknown.

This list might be added to somewhat, and certainly many more differences would appear were the dentitions better known, but none of the distinctions seem to be of a very fundamental nature. It is apparent that all four species are closely related. *Bolodon crassidens* and *B. elongatus*, imperfect as they are, seem definitely less like *Ctenacodon laticeps* than is *B. osborni*. We might therefore be justified in the hypothesis that the latter is the upper dentition of one of the Purbeck species referred to *Ctenacodon*. Since it is 50 per cent. larger than *Ctenacodon* uppers from the Morrison, and since *C. falconeri* is 50 per cent. larger than *Ctenacodon* lowers from the Morrison, it is possible that *Bolodon osborni* is the upper dentition of *Ctenacodon falconeri*, but this is only a reasonable possibility, backed by no conclusive evidence.

As for *Bolodon crassidens* and *B. elongatus*, they are at least specifically and perhaps generically unlike each other and equally unlike the other two species.

Greater refinement in the classification of the group and the correct association of upper and lower jaws must await the discovery of better material.

Bolodon crassidens Owen.

(Pl. III, fig. 7 ; Text-figs. 10–11.)

1871. *Bolodon crassidens* Owen, "Fos. Mam. Mesozoic," p. 54.
See also Lydekker, 1887, p. 203 ; Osborn, 1888A, p. 210.

Diagnosis.—No heels on P^{1-3}. P^3 with three tubercles and about same size as P^{1-2}. Ratio $\frac{P_4}{P_3}$=1·58. P_4 with but two distinct outer cusps and no true cingulum.

Formation and Locality.—Purbeckian of Durdlestone Bay, Swanage, Dorset.

Material.—The following specimen is in the British Museum.

47735. Most of right premaxilla and maxilla, with roots of I^{1-2} and crowns of I^3 and P^{1-4}. Holotype and only specimen. Figd., Owen, 1871, pl. iii, fig. 5. The anterior part of Osborn's composite figure (1888, pl. ix, fig. 16) is also largely based on it. (*Beckles Colln. Purchased* 1876.)

Dentition.

Incisors.—The apparent absence of I^1 in *Bolodon* has been cited as a possible difference from the American forms ; but this tooth was, in fact, present and is represented by its root. It is smaller than either I^2 or I^3 and is just antero-internal to

the former. The root is elliptical, its longer axis running from antero-external to postero-internal.

I^2 was already broken off near the apex when figured by Owen and Osborn, but at present it is broken off at the alveolus. It appears to have had a posterior accessory cusp, as does the corresponding tooth of the American *Psalodon*. The single root is large, elliptical in section, with the longer axis nearly parallel to the longitudinal axis of the jaw, but a little more external anteriorly.

I^3 is well preserved and has a very peculiar crown quite different from anything known among American plagiaulacids. There is one main cusp, median in position, stout but sharply pointed. At the posterior end of the tooth is a minute accessory cusp, and there is a somewhat larger antero-external accessory cusp. These two small cusps are at two of the angles of the triangular crown, the third angle (antero-internal) not being marked by a distinct cusp, although a sharp curving ridge runs to it from the apex of the main cusp. The latter has an angulate appearance due to this ridge and to three other smaller ones, one passing postero-internally, and two passing postero-externally and enclosing a long concave lozenge-shaped surface. The enamel has slight vertical rugosities.

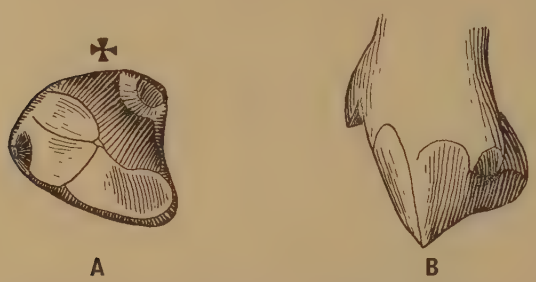


FIG. 11.—*Bolodon crassidens* Owen. Right I^3 of holotype. A, crown view. B, external view. The cross marks the external side. × 15 diam.

I^3 is followed by a short space, and then follows the closely crowded cheek series, the first four members of which are preserved.

PREMOLARS.—The first three premolars are almost alike in size and in structure, the first being a little smaller. Each has three cusps: one external, another of equal size internal and slightly posterior to the first, and a third (which is slightly smaller on P^1) anterior to the second and antero-internal to the first. There is a tendency to form a slight, cingulum-like ridge across the antero-external side of the tooth between the first and third cusps. The enamel is marked by distinct vertical furrows and is quite unworn, although the individual was not young. P^4, on the contrary, is much worn, the whole inner half being sheared off by wear against the trenchant lower premolars. It is half as long again as the preceding teeth and a little wider. Outside the shearing edge there remain two conical rugose cusps on the anterior two-thirds of the crown and behind these are traces of two or three small cuspules. Wear has removed all trace of the row of cusps which analogy with related forms would suggest to have once extended along the internal side and to have formed the original shearing edge. The shearing surface is not vertical, but passes upward and inward. P^5 and the molars are missing.

SKULL.

The premaxilla is a short, high element. The maxillo-premaxillary suture is almost vertical in the lower part, but curves backward somewhat above. The small

single infraorbital foramen is just anterior to the zygomatic root and above P^3. This root is formed by the zygomatic process of the maxilla, no trace of the jugal being seen, and arises above P^{4-5}.

The palate is not exposed and is probably not preserved.

MEASUREMENTS.

Maximum lengths in millimetres :

	I^2.	I^3.	P^1.	P^2.	P^3.	P^4.
47735	2·2	1·4	1·4	1·3	1·2	1·9

Bolodon osborni, sp. nov.

(Pl. III, fig. 6 ; Text-fig. 10.)

1888. *Bolodon crassidens* (*pars*), Osborn, *J. Acad. Nat. Sci.*, Philadelphia, IV, p. 265.

DIAGNOSIS.—No heels on P^{1-3}. P^3 but little smaller than preceding premolars, subquadrate, with an incipient antero-external tubercle. Ratio $\frac{P_4}{P_5}$=1·25. P_4 with three distinct cusps in the outer row and a cingulum external to them.

FORMATION AND LOCALITY.—Purbeckian of Durdlestone Bay, Swanage, Dorset.

MATERIAL.—The following specimen is in the British Museum :

47735*a*. Part of the right maxilla with P^1, the roots of P^2, P^{3-5}, and M^{1-2}. Holotype and only specimen. It has not been figured independently, but the posterior part of Osborn's composite restoration of *Bolodon crassidens* (1888, pl. ix, fig. 16) is largely based on it. (*Beckles Colln. Purchased* 1876.)

This specimen was not studied by Owen, but it is briefly mentioned by Lydekker (1887, p. 203), who based on it his assertion that *Bolodon* has three premolars and four molars. Osborn described the specimen in some detail (1888, pp. 210–211) agreeing with Lydekker as to the dental formula.

DENTITION.

PREMOLARS.—P^1 is much like that of *B. crassidens* : three sharp conical cusps of equal size arranged in an isosceles triangle, with the base internal and apex external. P^2 is missing, but was intermediate between P^1 and P^3 in size. It was implanted by two transversely elongated roots, the anterior a little wider, and this appears to have been the mode of implantation of P^{1-3} in all the known species of *Bolodon*.

P^3 is about 0·3 mm. shorter than P^1, from which it also differs in being lower, with less piercing cusps, and in being subquadrate rather than strictly triangular, with an incipient antero-external cuspule.

The following two teeth were considered by Lydekker and by Osborn to be molars, and this view is widely accepted. Osborn noticed that their function was different from that of the succeeding teeth and was very much puzzled by this fact,

which was not explained in a final way until Gidley's paper on *Ptilodus* (1909). We now know that this difference in function results from the fact that these teeth are opposed by the trenchant lower premolars, while the teeth behind them engage with the grinding lower molars. That the fourth and fifth cheek teeth must be considered as premolars is shown by the following facts:

1. They occlude with the posterior lower premolars, while the lower molars work against two teeth in back of them.

2. They are not truly molariform: their conical cusps, arranged less regularly than in the molars and without a straight longitudinal groove between the cusp rows, are those of typical premolars.

3. The beginning of the sort of elaboration which would lead from the simple triangular premolars to this more complex type is seen in P^3 of this same specimen.

4. The degree of protrusion from the alveoli on this specimen and on a well-preserved American one pertaining to *Ctenacodon labius* seems to show that these teeth fall naturally into the premolar and not the molar series in this respect.

The two teeth are of about equal size, the posterior one somewhat wider and longer. The shearing edge of P^4 is formed by a longitudinal row of four cusps, nearly central in position, which have not yet been removed by wear. External to these are three lower cusps, and around the anterior, external, and posterior sides of the crown is a distinct but not absolutely continuous cingulum.

P^5 of this species approaches P^4 of *B. crassidens* in size and character. The anterior part of the shearing edge shows traces of three cusps, and there was probably another posterior to them, now worn away. Outside and slightly anterior to the second and third cusps of the crest, respectively, are two smaller cusps, and outside these is a rugose and rather irregular cingulum, showing some tendency to form very tiny cingulum cusps. The posterior face of the crown bears a facet of wear distinct from that caused by the shear of the lower premolars and evidently due to the first lower molar when in its most anterior position.

Molars.—The true molars are only two in number, as in the lower jaw. The crown of M^1 bears two longitudinal rows of cusps, with three cusps in the outer row and four in the inner. The cusps are worn, especially the inner ones, and the original form is obscured. It seems probable that they were not simply conical, but were somewhat angulate or crested. There is a slight cingulum outside the antero-external cusp but not elsewhere. A tiny cuspule is seen on the inner side of the crown internal and slightly anterior to the postero-internal main cusp.

M^2 is a shorter, broader, subtriangular tooth. Its outer cusp row has two cusps and its inner three, and there is a prominent shelf-like extension external to the antero-external cusp. The postero-internal cusp, which is less worn than the others, seems to have its apex slightly inclined forward, as if representing a first stage in the development of the selenodont Upper Cretaceous ptilodontid type of upper molar.

The two molars are curiously placed with respect to each other. M^2 follows M^1 in such a way that the outer cusp row of the former continues the inner row of the latter. Osborn believed this to be due to crushing, and placed the molars directly

in line in his restoration, although recognizing the possibility that this peculiar lack of alignment was original. The fact that an uncrushed American specimen in the Yale Peabody Museum referred to *Ctenacodon* has M^{1-2} arranged in just the same way seems to indicate that the latter is the case. This is also indicated by the way in which the lower molars are worn in *Ctenacodon*. On M_1 the outer row of cusps fits into the groove of M^1 and consequently is much worn, while the inner row is nearly unworn on the apex because it occludes inside the upper tooth. On M_2 both rows are usually considerably worn, but the inner row, which fits into the groove of M^2, noticeably more so. Even the outer row is worn on the apex in this tooth because when the jaw is shifted forward at the beginning of the propalinal mastication it passes into the groove of M^1. The accompanying diagram (Fig. 12) makes these relationships clear.

This arrangement of the upper molars in the Plagiaulacidae also explains a

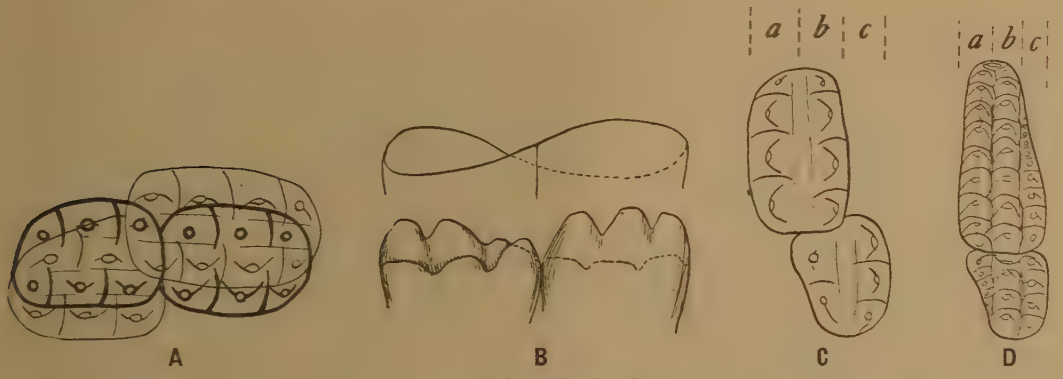


FIG. 12.—Diagrams of multituberculate molars. A, occlusion in a typical Upper Jurassic plagiaulacid, the lower molars indicated by the heavier lines. B, diagram to show the effect of wear on the relative heights of the two cusp rows in the left lower molars, internal view. C, crown view of right upper molars of an Upper Jurassic plagiaulacid, showing the arrangement of the cusps in three rows, although each molar has only two rows. D, similar diagram of molars of an Upper Cretaceous ptilodontid, showing the addition of a new *inner* row on M^1 and of a new *outer* row on M^2. Not to scale.

hitherto inexplicable peculiarity of the upper teeth of the Ptilodontidae and incidentally provides part of the strong evidence for the derivation of the latter from animals belonging or approximating to the former family. In the ptilodontids the upper molars have three rows of cusps, but in most of the genera one of the rows is incomplete. Curiously enough, the incomplete row, which has the appearance of a new cusp row just growing up, is not on the same side in the two teeth. In M^1 it is on the inner side of the complete cusp rows and appears at the posterior end of the tooth first, while in M^2 it is on the outer side and the anterior portion is the first to come into existence. Study of the accompanying diagram (Fig. 12) will show that the conditions in the plagiaulacids make this extraordinary feature of the ptilodontids not only natural but inevitable. Indeed, the beginning of this specialization is already seen in the present specimen, for the postero-internal cuspule on M^1 and the antero-external shelf on M^2 correspond in position to the new cusp rows developed by the later forms.

MEASUREMENTS.

Maximum lengths in millimetres:

	P^1.	P^2.	P^3.	P^4.	P^5.	M^1.	M^2.
47735*a*	1·5	—	1·2	1·5	1·8	2·0	1·7

Bolodon elongatus, sp. nov.

(Pl. III, fig. 8; Text-fig. 10.)

1871. *Bolodon crassidens* Owen (*pars*), "Fos. Mam. Mesozoic," p. 56.

DIAGNOSIS.—P^{1-3} elongated, with distinct posterior shelf-like heels not seen in any related form. P^3 smaller in proportion to the preceding teeth than in the other species of the genus.

FORMATION AND LOCALITY.—Purbeckian of Durdlestone Bay, Swanage, Dorset.

MATERIAL.—The following specimen is in the British Museum:

47736. Part of a badly crushed and broken skull with left P^{1-2} and right P^{1-3} preserved. Holotype and only specimen. Figd. (as *Bolodon crassidens*), Owen, 1871, pl. iii, fig. 6. (*Beckles Colln. Purchased* 1876.)

DENTITION.

The three premolars which remain in the specimen are of similar but not identical plan. Each has three main cusps, of which one is external and two internal. The latter are not quite symmetrical with respect to the first, the posterior one tending to be more directly internal and the other antero-internal. These cusps are stout but sharp and are of approximately equal size. Their enamel is rugose, as in the other species of the genus. The crowns of the teeth are elongated, instead of being rounded subequilateral triangles as in the other species, and behind the triangle of main cusps on each is a small, rounded, heel-like extension. This heel tends to develop two tiny cuspules, one external and one internal. These are so small as to be seen with difficulty, but they are clearly present at least on left P^1 and right P^2 and probably were present on the others also. The teeth decrease noticeably in size from P^1 to P^3.

SKULL.

The palate is complete between the first premolars and shows no vacuities here, although these may well have been present between the posterior cheek teeth. The palate is broad and the median suture is open. Much of the frontal and facial part of the skull is preserved, but the bones are mostly flat plates shattered into angular fragments and they reveal no important morphological characters.

MEASUREMENTS.

Maximum lengths in millimetres:

	P^1.	P^2.	P^3.
47736	1·9	1·8	1·4

Genus LOXAULAX nov.

Diagnosis.—Plagiaulacidae with outer cusps of lower molar shortened antero-posteriorly, subselenodont, four in number. Inner cusps three.

Genotype.—*L. valdensis*.

This new genus is made for the reception of *Dipriodon valdensis* Woodward, which, as shown under the heading of "Affinities" below, will not enter into any previously established genus. It is the only known definitely determinable lower Cretaceous mammal. The name is derived from λοξός, oblique, and αὐλαξ, groove, in analogy to *Plagiaulax*.

Loxaulax valdensis (A. Smith Woodward).

(Text-fig. 13.)

1911. *Dipriodon valdensis* Woodward, *Quart. J. Geol. Soc. London*, p. 278.

Diagnosis.—The only species of the genus.

Formation and Locality.—Wealden, Ashdown Sands, Hastings.

Material.—The following specimen is in the British Museum :

M 10480. A single molar, unworn and well preserved. Holotype and only specifically identifiable specimen. Figd., Woodward, 1911, Text-fig. (*Presented by Revs. P. Teilhard and F. Pelletier, S.J.*, 1912.)

This unique tooth has been clearly and accurately described by Woodward. It agrees closely in general form and in cusp arrangement with a left lower first

Fig. 13.—*Loxaulax valdensis* (Woodward). Views of holotype lower molar. A, crown view. B, external view. C, end view. All × 14 diam. Lower Cretaceous, Wealden, Hastings.

molar of *Ctenacodon*, and it is a reasonable hypothesis that this was its correct position in the dentition. Thus oriented, it has two longitudinal cusp-rows, with three cusps in the inner row and four in the outer. The outer cusps are lower than the inner, as appears always to be the case in first lower plagiaulacid molars. The anterior of these external cusps is far the largest and is subquadrate in outline. Behind it follow three (rather than two as in Woodward) cusps of decreasing size, the last very small, all short antero-posteriorly but as wide transversely as the first cusp. The first three of these cusps are distinctly subcrescentic, with the concavity of the crescents posterior. The latter fact strengthens the evidence for the orientation here adopted, for this is just the condition of the outer cusps in lower molars

of ptilodontids. The last cusp is like a small transverse crest (again, a similar last cusp is usually seen in ptilodontids).

The inner cusps differ from those of M_1 of *Ctenacodon minor* in the distinct presence of three cusps of nearly equal size, but they are very like those of *C. serratus* or of *C. scindens*. As in the last two species, the two anterior cusps have connate bases and their apices are separated only by a small notch, while the posterior cusp is larger and stands quite alone. The latter is subcrescentic, with the concavity of the crescent facing toward the mid-groove. This, again, is true also of the more complex postero-internal cusp of the ptilodontid first lower molar.

There is a narrow, cuspless shelf in front of the antero-external cusp.

The apparent cuspule on the anterior slope of the antero-internal cusp, seen in Woodward's figure, is not original but is due to slight cracking of the tooth here.

Affinities.

This tooth was originally referred to the genus *Dipriodon* on the basis of expediency, A. Smith Woodward clearly recognizing at the same time that its closer affinities were with the Jurassic forms, and not with those of the Upper Cretaceous as his reference to an Upper Cretaceous genus would seem to imply. As a matter of fact, *Dipriodon* is truly gigantic in comparison with the Wealden form, and its lower molars with their many highly crescentic and complicated crested cusps are so different from this primitive tooth that it is quite impossible, even for the sake of expediency, to retain them in the same genus.

The molar from Hastings is not, in fact, very different from the corresponding tooth in the American species of *Ctenacodon*. It differs chiefly as follows:

1. The cusps are more nearly selenodont.
2. The outer cusps are shorter antero-posteriorly.
3. There are four outer cusps and these are preceded by a cuspless shelf.
4. The inner cusps are more separate than in most specimens of *Ctenacodon*, but not more so than in the type of *C. scindens*.

These differences make it possible and necessary to place the present tooth in a distinct genus. It is of great interest that the differences from *Ctenacodon*, especially the tendency to increase in number of cusps and the incipient selenodonty (even in its details) mark definite progress in the direction of the later ptilodontids. *Loxaulax* is not a ptilodontid, however, but a progressive plagiaulacid.

? Loxaulax sp.

Formation and Locality.—Wealden, Ashdown Sands, Hastings.

Material.—In the British Museum:

M 10481. A fragment of a broken molar tooth. (*Presented by Revs. P. Teilhard and F. Pelletier, S.J.*, 1912.)

This fragment was mentioned by Woodward (1911) but has never been figured or described. It consists of about one-third of a molar tooth, apparently the anterior

end, and is sufficiently like *L. valdensis* to be referred to the same genus, although it is probably not homologous with the genoholotype.

One side of the tooth bears a large, rather blunt, complete cusp, and behind it another similar but higher one broken through the middle. Opposite these are two slightly higher and more slender cusps, their bases connate, and the whole compressed transversely. These cusps might correspond to the antero-internal ones of *L. valdensis*, but they are more compressed transversely, and the antero-external cusp extends to the anterior edge of the tooth, whereas it is preceded by a narrow shelf in *L. valdensis*, and it is here succeeded by a larger and higher cusp instead of by a smaller and lower one as in the latter. The tooth is also smaller, at least anteriorly, than is the genoholotype, measuring only about 1·1 mm. in anterior width.

Plagiaulacidae Indet.

1893. *Bolodon* sp., Lydekker, p. 281.

FORMATION AND LOCALITY.—Wealden, Hastings.

MATERIAL.—The following specimen is in the British Museum :

M 5691. A single broken lower incisor. Figd., Lydekker, 1893, fig. 1. (*Presented by Sir John Evans.*)

This is a rather stout tooth, 2·4 mm. in antero-posterior diameter, curved in an arc of a circle. The exposed face is probably the median one and is slightly convex. Antero-medianly there is a longitudinal angulation separating this face from the anterior one. The anterior and external faces are continuous with each other and are strongly convex. Most of the internal face is devoid of enamel, the latter extending on to this face to a line about 0·3 mm. from and parallel to the angulation above mentioned. The extent of the enamel on the outer face of the tooth cannot be made out. The bevelled, rodent-like end of the tooth is not original but is a broken surface.

The tooth is quite surely multituberculate, for no other animals with teeth of this type are known earlier than Upper Cretaceous. It is not an upper tooth, and hence should not be referred to *Bolodon*, for multituberculate upper incisors do not have long curved crowns or roots. It does not agree exactly with any lower incisors referred to *Ctenacodon* or to *Plagiaulax*, for these always taper more rapidly and, so far as known, have the enamel differently distributed. It may possibly belong to *Loxaulax*, although apparently too large for *L. valdensis*. The tooth is, in fact, not generically determinable.

Plagiaulax dawsoni, A. Smith Woodward.

1891 (1892). *Plagiaulax dawsoni* Woodward, *Proc. Zool. Soc. Lond.*, p. 585.

FORMATION AND LOCALITY.—Wealden, Wadhurst Clay, Hastings.

MATERIAL.—In the British Museum :

M 13134. A single badly worn and broken molar tooth. Holotype, figd. Woodward, 1891, text-fig. (*Presented by C. Dawson, Esq.*)

The enamel is all worn off this crown except around the edges, and all that remains is an irregular ovate basin with a rim of varying height, supported by two roots which are connate for some distance below the base of the crown. The tooth is comparable only with equally worn teeth of *Plagiaulax* and it is probably Plagiaulacid, although its generic and specific affinities are quite indeterminable.

Family PTILODONTIDAE Simpson.

Diagnosis.—Plagiaulacoids with premolars four above and two or one below, the last lower one shearing against the enlarged last upper one. M_1^1 much larger than M_2^2. Upper molars with three rows of cusps and the cusps, especially of M_1^1 much more numerous than in early forms, strongly crescentic and crested.

Discussion.—This family occurs in the European Cernaysian fauna (*Neoplagiaulax, Liotomus*) and is common in the American Upper Cretaceous and Paleocene. No doubt it also occurred in the European Upper Cretaceous although specimens have not yet been found. In all about eleven distinct genera, and perhaps more, are known and the family is far the best known of the Order. The differences from the Plagiaulacidae which these genera share and which define the family Ptilodontidae are in general such as could readily be due to evolutionary progress during the earlier part of the Cretaceous, and part of the evidence that this was what did occur has already been brought out in the preceding pages. The Plagiaulacidae are certainly very close to the ancestral stock of the Ptilodontidae. At the same time the gap between the two families is very real at present, and there are even several family characters which may point to a collateral rather than direct relationship. Of these the most striking is certainly the presence in the Jurassic forms of two upper shearing teeth of equal size, while in the Cretaceous and later forms there is but one shearing tooth and the preceding upper premolar is relatively simple in form and hardly to be derived from P^4 of the plagiaulacids. At least it is as yet impossible to adduce any evidence proving the derivation of the ptilodontids from the plagiaulacids *directly*, but the latter are certainly in most respects fair structural representatives of the Upper Jurassic stage of plagiaulacoid evolution, as we believe the ptilodontids to be fair structural representatives of the Upper Cretaceous and Paleocene stages.

Suborder *INCERTAE SEDIS.*

Family MICROCLEPTIDAE, nom. nov.

Synonym.—Microlestidae Marsh.

Diagnosis.—Rhaetic or Rhaeto-Liassic mammals known only from isolated teeth. The molars are oval and consist of a rounded, elongated basin, the sides of which rise into cuspidate ridges. The cusps are from eight to ten in number, and are of very different sizes on the same tooth.

Discussion.—This is one of the most troublesome and least known of mammalian families. It has long been designated the Microlestidae, but the name *Microlestes* (being preoccupied) can no longer be applied to any member of the group, so that in revising and redefining the family it seems best to make the new genus *Microcleptes* (for "*Microlestes*" *moorei*) the type. This genus is known from a relatively large series of well-preserved teeth the morphological characters of which are beyond question. To the family are referred, besides *Microcleptes*, *Thomasia* ("*Microlestes*") and the extremely questionable *Hypsiprymnopsis*.

The affinities of the Microcleptidae are painfully uncertain. Owen (1871, pp. 5, 10, 115) did not recognize any affinity with *Plagiaulax* but emphasized a fancied resemblance to *Myrmecobius* (with the supposedly primitive nature of whose degenerate teeth most of the earlier paleontologists were obsessed) and placed these forms in the same group with the pantotheres. Marsh (1887, pp. 332, 345) was the first to point out a resemblance between the molars of "*Microlestes*" and of the Plagiaulacidae and to refer the earlier forms to the Allotheria. Osborn (1888A, pp. 214–5) went even farther, referring the English Triassic species *M. moorei* to the Upper Jurassic genus *Plagiaulax* and placing "*Microlestes*" in the family Plagiaulacidae. Gregory (1910, p. 167) placed the forms now called *Hypsiprymnopsis*, *Thomasia*, and *Microcleptes* all in *Microlestes* and referred them to the Plagiaulacidae. Hennig (1922, p. 263) also inclines to this arrangement.

What is the evidence that the microcleptids are closely related to the plagiaulacids? It is all summed up by Gregory (1910, p. 167) as follows:

"(1) The *Microlestes* [*Thomasia*] *antiquus* molar while more elongate and compressed, resembles the second lower molar of *Plagiaulax* [*Ctenacocon*] *minor*, . . . in possessing a high antero-internal cusp on the raised internal border and a row of small external cusps. In both genera the molars have a median longitudinal basin and two roots.

"(2) The lower molar called '*Microlestes*' [*Microcleptes*] *moorei* comes from a formation from which only one other mammalian fossil is known: *viz.*, the type of *Hypsiprymnopsis rhaeticus* Dawkins. This is a grooved lower premolar of Multituberculate type."

The supposed identity between *Microcleptes* and *Plagiaulax* or *Ctenacodon* was based on a misconception of the latter genera, due to the poor preservation of the material then available. There is a certain resemblance, not too detailed, as both have elongated molars with cusps down each side; but molars in which the resemblance is not closer than that have very often arisen quite independently. *Ctenacodon*, with its six large cusps arranged in two parallel rows is fundamentally distinct from the microcleptids with their basined molars with more numerous cusps of very unequal sizes arranged about the curving rims. The resemblance is certainly not one on which to rely.

As for the evidence of *Hypsiprymnopsis*, it does *not* come from the same geological horizon as *Microcleptes* but is considerably older and, furthermore, it was probably not a shearing tooth at all, and if it were a shearing tooth it would have to be very unlike the plagiaulacid one. So that its evidence is negligible.

There is another point of evidence, first mentioned by Owen, which is negative but important, that is that no plagiaulacid shearing teeth were, in fact, found with the microcleptid molars. If *Microcleptes* had such teeth this would be almost impossible to explain, for these shearing premolars are (in *Ctenacodon*) twice as numerous as the molars. In the Purbeck and Morrison formations molars are extremely rare, and shearing teeth fairly common. It may be urged that the series is small, but surely in twenty-nine teeth, which is the number originally discovered by Moore, some of the more numerous premolars must occur, were they present in these animals. It cannot be supposed that they were present and overlooked, for even almost microscopic slivers of bone and piscine denticles were saved, and a plagiaulacid premolar is a very characteristic tooth which Moore would not possibly have failed to separate.

It is clear that the microcleptids cannot be placed in the Plagiaulacidae, and that it is by no means certain that they are related at all. It is equally doubtful whether they are really multituberculates or not. Rather distant and unconvincing as it is, the resemblance between microcleptids and plagiaulacids is much closer than between microcleptids and any other multituberculates. The most important multituberculate dental character is not the possession of many tubercles, for most mammals and some reptiles have just as many as at least the Jurassic multituberculates, but the arrangement of these tubercles in regular, longitudinal rows. This really diagnostic character is not well developed in the microcleptids, indeed is only slightly hinted at.

The microcleptid pattern is really unique. It does, to be sure, resemble some later ones such as that of certain fruit bats, as Matschie has shown, but this is clearly secondary. It is even open to question whether the microcleptids are mammals at all—the molars are about as much like those of some almost contemporary diademodonts as they are like those of the (much later) plagiaulacids. The only definite evidence of mammalian affinities is the divided nature of the roots. So far no mammal-like creature has yet been found which had divided molar fangs and which yet retained a reptilian lower jaw suspension. Such may have occurred, but so far as experience goes, root division and a squamoso-dentary articulation go together (they are certainly related phenomena) and we must assume that the microcleptids are mammals.

To sum up the inconclusive evidence as to the affinities of the Microcleptidae:

1. Having divided roots, they are probably more mammal- than reptile-like, and may be placed among the Mammalia.

2. They are so little known and what is known is so little like any other group of animals that they cannot be assigned to any particular mammalian group with any degree of confidence.

3. They show a distant resemblance to some multituberculates and may be placed in this Order, but with the understanding that there is no decisive evidence in favour of this view and that some facts oppose it.

Genus MICROCLEPTES nov.

1867. *Microlestes* Plieninger (*pars*), Moore, *Quart. J. Geol. Soc.*, London, XXIII, p. 487.

Diagnosis.—Microcleptidae having one rim of basined molar teeth with three tubercles, which are either subequal or with the anterior one smaller than the other two. The other side of the basin with a single large anterior cusp followed by three or four progressively smaller ones.

The name is derived from μίκρος, small, and κλέπτης, thief, and is meant to recall, in sound and in meaning, the preoccupied name under which this genus and *Plieningeria* were long united.

Discussion.—From a fissure deposit at Holwell, near Frome, Charles Moore obtained a very remarkable collection of fish, reptile, and mammal remains, mostly now in the Museum of the Bath Royal Literary and Scientific Institution (hereafter called the Bath Museum). Among the almost innumerable remains of lower animals —there are estimated to be 70,000 *Acrodus* teeth alone—he obtained twenty-nine mammal teeth. Of these only twenty have been available for the present research. In the Bath Museum are fifteen, including all of the ten figured by Owen. The British Museum has three, and the Peabody Museum, Yale University, has two. This leaves nine unaccounted for. According to a letter (now among the Marsh Papers in the Peabody Museum) Moore sent to Marsh on Sept. 27, 1881, nine mammal teeth. Two of these are the ones now in the Yale Collection, the other seven were not added permanently to this collection and their present location is quite unknown. Of the other two specimens of the twenty-nine nothing is known beyond Moore's simple statement that that number were discovered. These and the seven sent to Marsh but not retained by him may yet appear. Even if they are lost, this is not irretrievably unfortunate, for all of Owen's types survive and the known specimens include several essential duplicates of each sort, so that it is improbable that the missing specimens included any novelties.

The twenty specimens which have been studied include four different morphological types: three sorts of molars and a few (five) incisors or canines. Two of the molar types differ very definitely from *Thomasia*, and are made distinct species of a new genus, *Microcleptes*, while the third must be referred to *Thomasia*, and is made a distinct English species of that genus.

The forms here placed under *Microcleptes* have hitherto either been referred to *Plagiaulax* (Osborn) or to *Thomasia* ("*Microlestes*"—all other writers). It is true that almost every writer since Owen has stated that the English and German species probably were not truly congeneric, but no one has hitherto taken the necessary step of erecting a new genus for the former. That it cannot be referred to *Plagiaulax* is obvious, as has already been pointed out. It has significant resemblances to *Thomasia*, resemblances of a sort which lead one to believe that in certain cases homologous teeth are involved, but there is at least one constant and significant difference as follows:

Microcleptes.	*Thomasia.*
Three cusps of one side subequal, or anterior one smallest.	Anterior of three cusps the largest and others rapidly diminishing in size.

It is a legitimate criticism that classification on the basis here adopted may lead to placing different teeth of the same dentition in different species if they happen to be unlike. Convenience, however, demands that each type be given a name by which to call it. If other similar animals were known, it might be possible to unite these teeth into probable broad genera by analogy, but the Microcleptids are too isolated for this. Finally, each morphological type which is here recognized and given a specific name includes a number of teeth of different proportions, different number of roots, and somewhat different size—that is, includes teeth probably from different parts of the dentition of the same species; which considerably increases the chance that these are natural species. In our present state of fairly dense ignorance the present course seems the most practical.

Microcleptes moorei (Owen).

(Pl. I, fig. 4; Text-figs. 14, 15*c*.)

1867. *Microlestes* sp. Moore, *Quart. J. Geol. Soc.*, London, XXIII, p. 487.

1871. *Microlestes moorei* Owen, "Fos. Mam. Mesozoic," p. 6.

1888. *Plagiaulax moorei*, Osborn, *J. Acad. Nat. Sc.*, Philadelphia, IX, p. 214.

1910. "*Microlestes*" *moorei*, Gregory, *Bul. Amer. Mus. Nat. Hist.*, XXVII, p. 167.

1922. *Microlestes* (*Plagiaulax*) *moorei*, Hennig, *N. Jahrb. Min. Geol. Paläont., Beil. Bd.*, XLVI, p. 226.

Diagnosis.—Three subequal cusps on one side of molar crown, the large cusp of the other side followed by four smaller ones of which the last two are about equally prominent. The basin elongate and relatively narrow transversely.

Formation and Locality.—Rhaetic fissure deposit at Holwell, near Frome, Somerset.

Material:

a. In the Bath Museum:

M 211. Molar. Figd., Owen, 1871, pl. i, fig. 6. Lectoholotype, one of Owen's syntypes.

M 212. Broken molar. Figd., Owen, 1871, pl. i, fig. 11. One of Owen's syntypes.

M 213. Molar. Figd., Owen, 1871, pl. i, fig. 5. One of Owen's syntypes.

M 214. Molar. Figd., Owen, 1871, pl. i, fig. 9. One of Owen's syntypes.

M 215. Molar. The reference of this specimen to this species rests on Owen's figure. The specimen is now almost impossible to make out. Apparently the roots have been broken off and the crown is not exposed as now preserved. Figd., Owen, 1871, pl. i, figs. 1–4. One of Owen's syntypes.

M 216. Molar. Figd., Owen, 1871, pl. i, fig. 7. One of Owen's syntypes.

M 217. Molar. Figd., Owen, 1871, pl. i, fig. 12. One of Owen's syntypes.

M 222. Molar. Figd., Owen, 1871, pl. i, fig. 8. One of Owen's syntypes.

b. In the Peabody Museum, Yale University: 13622A: Molar.

Description.

This species was described by Owen on the basis of ten teeth (M 211–M 219 and M 222 in the Bath Museum). None of these was selected as type and they must therefore be treated as syntypes. As they do not all agree among themselves it becomes necessary to choose a lectotype. Ordinarily the first specimen figured by Owen would be chosen, but the present condition of this specimen (M 215) is so unsatisfactory that it seems best to select M 211, a well-preserved, well-displayed tooth typical of the majority of Owen's types. Of the original cotypes, two do not agree sufficiently closely to be included in this species; one, M 218, is either a canine or an incisor, and is listed as *Microcleptes?* sp., the other, M 219, is made the type of a new species of *Thomasia*. The present description is based on all the specimens, but especially on the lectotype and on the Peabody Museum specimen, which closely resembles the type and is peculiarly suitable for detailed study.

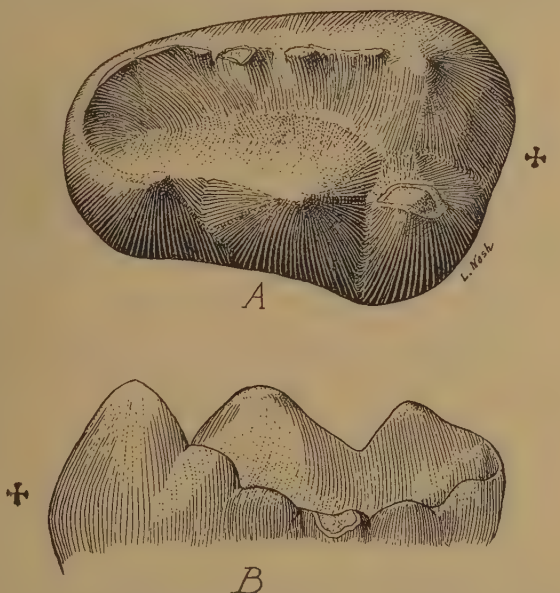


Fig. 14.—*Microcleptes moorei* (Owen). Molar, Yale Peabody Museum Cat. No. 13622A. A, crown view. B, side view. × 30 diam. Rhaetic, Holwell, Somersetshire.

The contour of the tooth, in crown view, is somewhat irregularly oval (not elliptical)—it is elongated, rounded, with one end wider than the other. This wider, higher end will be called the anterior one, for purposes of convenience in description. There are here two stout cusps placed directly opposite each other. The larger of these two cusps, which is the largest cusp on the tooth, is continued posteriorly by a ridge the top of which is divided into four cusps of equal prominence. The anterior three of these small cusps decrease regularly in height from first to third; the third and fourth are of about the same height.

The other side of the tooth is also bordered by a longitudinal row of cusps, but here they are three in number and of nearly equal size, although the middle one is slightly the largest. It is nearly as large as the anterior cusp of the other series. The sides of these three cusps which slope away from the basin of the crown are markedly convex, and the cusps are here separated from each other by distinct vertical grooves below the notches which separate their apices. The other side of the anterior cusp is also convex, and this cusp is nearly conical. The slopes of the other cusps which pass down into the basin are nearly straight in horizontal section, slightly concave in vertical section, and the bases of the two cusps are hardly distinguished from each other below the notch on this side.

Between these two cusp-rows, on the posterior two-thirds of the tooth, is a long narrow basin. On one side it is bounded by the more posterior two of the three subequal cusps, on the other by the three posterior ones of the four small cusps which follow the largest one. At the posterior end the basin is closed by a low ridge which curves round from the end of one row to the other. In some specimens this ridge is not apparently cuspidate, in others, such as the Yale specimen, it forms a fairly distinct, obliquely elongated cusp just posterior to the four small cusps. Anteriorly, the floor of the basin rises more gradually and its true anterior end is marked by the saddle between the two large opposite anterior cusps, the bases of which are confluent.

There is a distinct tendency to form a shelf or cingulum anterior to this saddle, along the anterior face of the tooth. This may be very obscure, as in the Yale specimen, or quite distinct, as in the holotype.

There is considerable variation in the size, proportions, and minor characters of the molars which may be assigned to this species. These variations are probably due in large part to the position of the tooth in the dental series. M 211 measures 2·4 mm. by 1·8 mm. and most of the specimens are within the limits of error (in measurement of such minute teeth) of being the same. Y.P.M. 13622A, however, measures slightly less, 2·2 mm. by 1·55 mm. M 217 is remarkably small, measuring only 1·7 mm. in length, as preserved.

This last tooth is also unusual in other ways. It is remarkably narrow, and is more triangular than the typical teeth. The ridge which follows the larger anterior cusp is not distinctly cuspidate. The smaller size is probably original, but it is quite possible that the other differences are due to wear or breakage.

M 217 has two roots, one at each end. M 213 has three roots, two at the broader end and one at the narrower end. The single root is somewhat broadened transversely, and, as it is very slightly grooved vertically, it is possible that it divided into two at a point beyond the part preserved. The four smallest cusps on this tooth are small and indistinct, the anterior cingulum faint. The external bases of the two anterior cusps of the row of three are swollen in such a way as to make them almost faintly cingulate. M 211 has two equal fangs according to Owen (they cannot now be seen), and the same is true of M 216 and of M 214. M 215 originally had four nearly equal roots. These differences in root number are undoubtedly due to position in the jaws, as they are accompanied by no important changes in coronal characters.

Owen's figures and descriptions give a very erroneous conception of at least two of the specimens, and it is necessary to correct this. M 216 (Owen, 1871, pl. i, fig. 7) is made to appear as if it had three cusps down one side and four smaller subequal cusps down the other, with a rectangular basin between them. The tooth is very worn and rather vague, but the structure is that normal for this species, save that the cusps are truncated by wear. The side which bears four subequal cusps in the figure really has one large one at the end followed in the usual manner by four smaller ones.

M 212 (Owen, 1871, pl. i, fig. 11) is figured and described as being remarkably

short and having but one root. This is quite true, but the cause is that the two large, opposite anterior cusps, with their supporting root or roots, have been broken away. If these were preserved the tooth would be perfectly normal for this species.

ORIENTATION.—The orientation of these isolated teeth has been much discussed, but it presents insuperable difficulties at present. The molar with four fangs and that with three were called upper molars by Owen; the others he called lower molars. In the case of the four-fanged tooth he considered the row of three cusps to be internal, and the end which I have called anterior, posterior. In dealing with M 213, however, which also he considered to be an upper molar, he called this the anterior end. In dealing with the teeth which he regarded as lower molars, he always referred to the larger end as the anterior one, as I have done, and considered the row of three subequal cusps to be external. On this basis M 211 would be a right lower molar. Owen, however, gave no grounds for these orientations. He was not consistent, moreover, for in dealing with the type of *Thomasia*, which is sufficiently like *Microcleptes* for the homologies of the various cusps to be free from doubt, he still made the row of three cusps external, but made the more prominent end of the tooth posterior. This would make this tooth a right lower molar, whilst the orientation which he adopted for *Microcleptes* would make it a left lower. Osborn also made this tooth a right lower molar (1888A) but changed the orientation entirely, for he considered the row of three to be internal and the more prominent end anterior. This was based on the supposed resemblance to *Plagiaulax*.

Branca (1915) adopts the same orientation as Osborn for *Thomasia* (the orientation of this genus and of *Microcleptes* being really the same problem, they will here be discussed together). His argument is rather too elaborate to reproduce in full. He supposes it to be a lower, since multituberculate uppers are said usually to have three rows of cusps in the uppers—this is not true, as all Upper Jurassic forms have only two rows in the uppers, and in any event it remains to be shown that the microcleptids are multituberculates. He also supposes that the smaller number of cusps is usually in the inner row and that the largest cusp is often anterior—statements also open to exception as to truth and as to analogy. His statement that the tooth is a left lower molar is an obvious *lapsus calami;* his own argument would make it a right lower.

Hennig (1922) discusses previous conceptions of orientation without committing himself to any, and it is advisable to follow him in this cautious stand. Even if the microcleptids prove to be multituberculates, which is very uncertain at present, they are so unlike any other known forms that arguments from analogy have no value whatsoever. The calling of the more prominent end "anterior," is merely a convention intended to assist in pointing out homologies and to make description a little less clumsy. It is not advocated as the necessarily correct orientation. In all the accompanying figures of microcleptids this conventional "anterior" end is marked with a cross.

Microcleptes fissurae, sp. nov.

(Pl. II, figs. 2–3 ; Text-figs. 15*a–b*.)

DIAGNOSIS.—Three cusps on one side, of which the most anterior is much reduced. The large cusp of the other side followed by only three distinct small cuspules and then by an obscurely cuspidate ridge curving around the posterior end of the tooth. The basin relatively much broader than in the other species.

FORMATION AND LOCALITY.—Rhaetic, filling fissure at Holwell, near Frome, Somerset.

MATERIAL.—All the material is in the British Museum.

M 2401A. Molar. Holotype. (*By exchange with the Bath Institute*, 1884.)
M 2401B. Molar. This tooth is broken. Reference to this species is probable but not certain. (*Same History*.)
M 2401C. Molar. (*Same History*.)

DISCUSSION.—Despite the fact that these molars are stated by Lydekker (1887, p. 203) to agree with those figured by Owen, it is a curious fact that they differ from

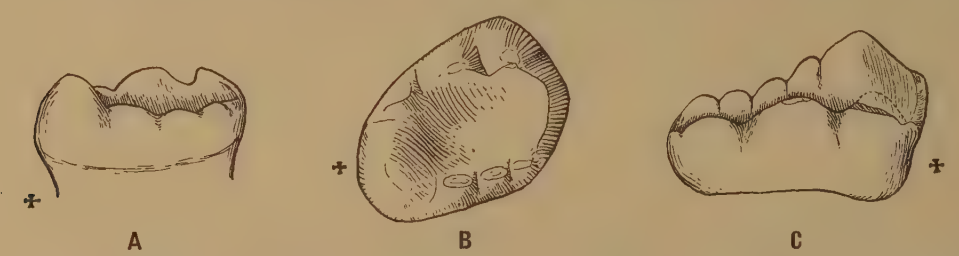


FIG. 15.—*Microcleptes fissurae* Simpson and *M. moorei* (Owen). A, *M. fissurae*, side view of holotype. B, crown view of same. C, *M. moorei*, side view of lectotype. All × 15 diam. Cross-marks conventional anterior end. Rhaetic, Holwell, Frome, Somersetshire.

any in the Bath Museum, and yet agree very well with each other. The chief differences from the teeth here referred to *M. moorei* have been brought out in the brief diagnosis above, and can be seen in the figures. Instead of having two large cusps of nearly equal size at the anterior end, the anterior cusp of the row of three is much reduced and is rather inconspicuous. The middle cusp of this row is the largest, as in *M. moorei*, and the posterior one only slightly smaller. The anterior cusp of the other row is large and blunt, and the reduction of the cusp opposite makes it occupy a position more median on the tooth than in *M. moorei*, so that it alone forms almost all of the anterior rim of the basin. It is followed by only three distinct cusps instead of four, although the ridge which curves around the posterior end of the tooth is obscurely cuspidate, and its end may simulate a fourth cuspule of this series. The basin is broader, more open, less elongate than in *M. moorei*.

The holotype measures 2·0 mm. in length by about 1·5 mm. in width, and M 2401C measures 2·1 mm. by about 1·6 mm.

? Microcleptes sp.

FORMATION AND LOCALITY.—Rhaetic fissure filling, Holwell, near Frome, Somersetshire.

MATERIAL.—The following specimens are in the Bath Museum:

M 218. A canine or incisor. Figd. as canine of *Microlestes moorei*, Owen, 1871, pl. i, fig. 13.

M 220. Four canines, or incisors, or both.

DESCRIPTION.—With the molars here assigned to *Microcleptes moorei*, *M. fissurae*, and *Thomasia anglica*, Charles Moore found several one-rooted, simply pointed teeth of which five are preserved in the Bath Museum. There were probably others among the nine teeth which have disappeared. These small thecodont teeth are quite mammalian in aspect, and their association with *Microcleptes* makes it probable that they belong to this genus, although of course this is not proven.

M 218 is a curved tooth, tapering to a rather blunt point at each end. It is somewhat compressed laterally, and is a good miniature of a typical carnivorous canine. Enamel seems to cover an unusually large proportion of the tooth, about two-thirds. Owen did not hesitate to call this a canine, and indeed an upper canine, but of course if the microcleptids are multituberculates, and if these teeth really belong to them, then it must be a lower incisor. Certainly it is more like a canine than a multituberculate incisor, but it is impossible to affirm that it could not be the latter.

The other specimens are, if anything, even less like the typical multituberculate incisor. They do not in any case have the well-defined, flattened median face of the latter, and the enamel (which in these specimens covers a much smaller proportion of the tooth than in M 218) is distributed as it would be on a canine, and not as it usually is on a multituberculate incisor.

GENUS HYPSIPRYMNOPSIS Dawkins.

1864. *Hypsiprymnopsis* Dawkins, *Quart. J. Geol. Soc.*, London, XX, p. 406.

1871. *Microlestes* (*pars*) Owen, "Fos. Mam. Mesozoic," p. 8.

DIAGNOSIS.—A single tooth, long and narrow, implanted by two roots, and with four or five tubercles along the crest. The original was probably broken.

GENOTYPE.—*H. rhaeticus*, Dawkins.

Hypsiprymnopsis rhaeticus Dawkins.

1864. *Hypsiprymnopsis rhaeticus* Dawkins, *Quart. J. Geol. Soc.*, London, p. 406.

1871. *Microlestes rhaeticus* Owen, "Fos. Mam. Mesozoic," p. 8.

DIAGNOSIS.—The only species of the genus.

FORMATION AND LOCALITY.—Lowest Rhaetic, near Watchet, Somerset.

MATERIAL.—None, the unique original having been lost.

DISCUSSION.—The one specimen of *Hypsiprymnopsis* has suffered the fate which has overtaken so many Rhaetic mammal teeth—it has mysteriously vanished.

Deposited in the Geology Department of the University Museum, Oxford, by the discoverer, Sir William Boyd Dawkins, the specimen has disappeared. This is especially unfortunate since it appears to have been the oldest known mammal (with the possible exception of *Tritylodon*) and since there are important doubts as to its characters which only further study could have illuminated. All that can now be done is to quote the published descriptions.

The original description by Dawkins follows :

" The crown, . . . oblong in shape, is very long in proportion to its width, being 1·5 inch long to 0·4 wide [see below]. The higher side of its obliquely worn summit, imbedded in, or rather adherent to, the stone, exhibits two isolated involutions of enamel on that portion of the tooth that is supported by the posterior fang. Anterior to these are two wider and less prominent folds. The anterior corner, unfortunately broken by the waves, may perhaps have borne an additional fold. The cervix is very well defined. Of the two divergent fangs, the anterior had been broken short off before it was imbedded in the matrix ; the posterior or smaller of the two (in length 0·11 inch) is perfect, and has its tip slightly reflected. . . ." Dawkins considered the tooth to be a trenchant premolar and compared it with premolars of *Hypsiprymnus* and of *Plagiaulax*. According to Dawkins' figure the length would really be about 4·4 mm.

In his description of this specimen (1871, p. 8) Owen quotes Phillips, and it is probable that Owen had not himself seen the specimen. He also mentions a figure by Phillips, and this may have been the basis for the new figure given by Owen (1871, pl. i, fig. 16). The more significant portions of Owen's discussion may be extracted (the phrases within the secondary quotation marks are from a letter of August 29, 1870, from Prof. Phillips to Prof. Owen) :

" The crown, as in *Microlestes*, is very short in proportion to its fore-and-aft width, being one line ($\frac{1}{12}$th in.) in height at the bifurcation of the two fangs and 2 lines ($\frac{1}{6}$th in.) from the front to the hind border. . . . The breadth or transverse diameter of the tooth cannot be accurately determined, for the side imbedded is ' entirely concealed ' and the side exposed to view has been subject to attrition, presenting a ' smooth polished surface, which extends without interruption from the crown into the fangs,' and exposing ' a dark band . . . crossing what would be called the base of the crown.' This part of the base shows ' four grooves passing downwards from the crown towards the fangs.' . . . The higher side of the tooth . . . is the thick enamelled border of a low crown bounding the inner side of a pounding surface which was depressed, flat and smooth in the centre. This coronal border . . . was disposed in four, probably five, tubercles ; on the latter alternative the fifth is broken away, most likely as being the largest and most prominent. The attrition of the masticatory tubercles of the preserved border of the crown of this little molar has exposed the dentine. ' The crown of the tooth,' writes Prof. Phillips, ' is obliquely worn, and on the worn surface are little cusps, as in my figure, also worn, but a little projecting at the edges . . . as they were formed of enamel and dentine within the general border of enamel.' . . ."

Owen goes on to show that the resemblance to *Plagiaulax* or to *Hypsiprymnus*

is not close, in which one must agree. His interpretation of the tooth is that it represents one side of a *Microcleptes* molar with the large anterior cusp and the other row of three cusps broken away. From Dawkins' figure and description and that given by Owen, the two agreeing very well, it is seen that this is a very reasonable explanation. If a *Microcleptes moorei* molar of the two-rooted variety were mutilated in the way suggested it certainly would look almost exactly like *Hypsiprymnopsis* as figured. There are difficulties however. Phillips does not speak of a broken face but of a smooth one, polished by wear. *Hypsiprymnopsis* is notably larger than *M. moorei*. Finally, Owen had not seen the original, whereas Dawkins, who had seen and studied it, was led to an opposite conclusion. On the other hand, we cannot agree with Dawkins that the tooth resembles a premolar of *Plagiaulax*—it is very different.

In the face of these conflicting opinions and the impossibility of choosing between them now that the specimen is lost, there is no choice but to retain this fossil under its original name and to realize that *Hypsiprymnopsis rhaeticus* is a form of doubtful morphology and indeterminate affinities.

Genus THOMASIA Poche.

1847. *Microlestes* Plieninger, *Jahresh. Ver. vaterl. Naturk. in Württ.*, p. 164.
Non Microlestes Schmidt-Goebel, 1846, *Helfer's Samml.*, I, p. 41.
1908. *Thomasia* Poche, *Zool. Ann.*, II, p. 269.
1919. *Plieningeria* Krausse, *Arch. Naturgesch.*, LXXXIII, (A), 6, p. 50.

Diagnosis.—Microcleptidae with one rim of basined molar teeth with three tubercles of which the anterior is markedly the largest and the posterior one may be much reduced. The anterior cusp of the other side is not as high as that just mentioned, and is followed by four or more smaller cusps, the most posterior of which forms part of the posterior closure of the basin.

Genotype.—*T. antiqua* (Plieninger).

This is the genus long known as *Microlestes*. Poche (1908) and Krausse (1919) have recently shown, however, that the name *Microlestes* is preoccupied and they have proposed to replace it, the former by *Thomasia*, the latter by the very fitting name *Plieningeria*. *Thomasia* has priority and is the valid name of the genus. Besides the genotype, *Thomasia antiqua*, there is here recognized an English species, *Thomasia anglica*, quite distinct from *M. moorei*, which was long considered congeneric with *T. antiqua*, but which is now placed in a distinct genus. It is obvious that *Thomasia* and *Microcleptes* are closely related, and their various cusps may be homologized without much question, but they are readily distinguishable generically.

Thomasia antiqua (Plieninger).

(Text-fig. 16.)

1847. *Microlestes antiquus* Plieninger, *Jahresh. Ver. vaterl. Naturk. in Württ.*, p. 164.
See also Lyell, 1855, p. 342; Owen, 1871, p. 3; Osborn, 1888A, p. 214; Branca, 1915, p. 19; Hennig, 1922, p. 192.

Diagnosis.—Posterior cusp of the row of three small but distinct. Anterior cusp of the other row preceded by a well-marked minute basal cusp and followed

by three well-differentiated small cusps and then by a fourth which is obscurely bifid, and curves round the posterior end of the basin. Length about 2 mm.

FORMATION AND LOCALITY.—From a Rhaeto-Lias Bonebed, probably from the Schlösslesmühle, Württemberg.

MATERIAL.—*a*. In the Stuttgart Naturalienkabinet. Single molar. This is the holotype (but see below). Figd., Hennig, 1922, pl. ii, fig. 9, and also Plieninger, 1847, pl. i, fig. 3 ; Lyell, 1855, fig. 441 ; Osborn, 1888A, fig. 7, 1 ; Falconer, 1857, fig. 16 ; Owen, 1871, pl. i, fig. 14–15 ; Branca, 1915, fig. 16.

b. In the British Museum :

M 13135. Two casts of the above specimen. (*Presented by Sir Charles Lyell.*)

DISCUSSION.—This species has been so very fully described and discussed recently (Branca, 1915 ; Hennig, 1922) that only a brief notice need be included here for purposes of completeness and for comparison with the better known English material.

As with most of the Württemberg Rhaeto-Lias mammal teeth, the history of the type-material of *Thomasia antiqua* is rather confused. The original locality is unknown, Plieninger stating only that the two mammal teeth and *Sargodon tomicus* were from near Degerloch and Steinenbronn. In the English literature only the first locality is usually mentioned, and it has been transmuted into Diegerloch and finally Diederloch. Hennig considers the locality to have been the Schlösslemühle, which is near Steinenbronn. Original lithographic figures from four aspects were given by Plieninger. Lyell gave two original figures which he obtained from H. von Meyer. Falconer (1857) gave a wood-cut, perhaps based on Lyell, which is made into a lithograph in his collected memoirs (vol. II, pl. xxxiv, fig. 7). Osborn gave new line engravings of three aspects, from drawings furnished by E. Fraas. Finally Branca has given very clear half-tones of drawings of four aspects, and Hennig has given a similar new figure of the crown aspect. Making due allowance for the inevitable personal idiosyncrasies of the artists, the differences in technique, and the different optical instruments available, these illustrations all agree very well. They show cusps of the same number, arranged in the same way, and of the same relative heights. One important difference they do show : in Plieninger's drawings, in Branca's crown view, in Osborn's end view, and to a somewhat less degree in the crown views of Lyell and Osborn, the two rows of cusps appear to be separated by a narrow groove with a sharp bottom, while in Branca's end view and Hennig's crown view it is seen that they are actually separated by an elongated basin with a rounded bottom. As a matter of fact, the tooth is unquestionably basined, as are all microcleptid molars, although the basin is not broad and open as in *Microcleptes fissurae*, for instance. The lighting and other variable or subjective factors readily account for the differences in the drawings—as is well attested by the fact that one of Branca's drawings, made by the same worker, shows a basined crown and another does not. The same is true to a less striking degree of the drawings furnished to Osborn.

As Hennig has pointed out, there are also puzzling differences in the verbal descriptions published by these several students. He has even raised the question whether the tooth studied by Plieninger was the same as that studied by later workers, but the agreement in the figures seems to confirm the identity. We also find that the measurements given by Plieninger are 50 per cent. too large to apply to the present specimen; but as Hennig points out, even such a large variation may have little significance in dealing with material so small and difficult of measurement. There is a cast in the British Museum which was made in Plieninger's time, and which must represent the original; a very accurate measurement of the length obtained from it agrees, not with Plieninger's measurement, but with Hennig's.

As a final difficulty, we read in Branca that after the return of the specimen to Stuttgart "ist er später hingefallen und dabei zerstrümmmert worden." When, however, Hennig came to look through the exhibition series of the Naturalienkabinet a few years later, he found a specimen which agrees so exactly with that described by Branca (save in the matter of the basin, which has already been discussed) that

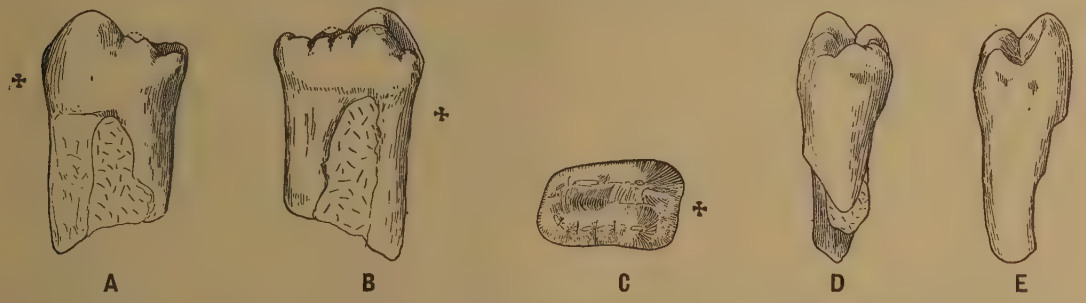


FIG. 16.—*Thomasia antiqua* (Plieninger). Holotype molar. A, side view. B, other side. C, crown. D, conventional posterior end. E, conventional anterior end. All × 10 diam. Cross marks conventional anterior end. Rhaeto-Lias, Württemberg.

it is impossible not to accept his view that it is the original, despite the clear statement of its loss.

The morphology of the tooth now preserved at Stuttgart is simple, and does not differ very greatly from that of *Microcleptes*. At one end are the two largest cusps, placed opposite each other and differing from those of the latter genus in that it is the one which belongs to the row of three cusps which is here the larger of the two. It is followed by two other cusps as in the other genus, but these, instead of being about equal to it, or even larger, are progressively much smaller. The other anterior cusp is preceded by a small cuspule, a sort of homologue of the slight anterior cingulum of *Microcleptes*, and is followed by two distinct cusps in the same longitudinal row but smaller. These are followed by a ridge which continues this rim around the posterior end of the tooth, and which is rather obscurely bifid, so that it may be thought of as adding two more posterior and more median cusps to this series. As in *Microcleptes moorei*, the narrow elongated basin is closed posteriorly by this ridge and anteriorly by the saddle between the two large anterior cusps. The low crown is implanted by two roots, of which the posterior one is slightly the larger.

Thomasia anglica, sp. nov.

(Pl. II. fig. 4; Text-figs. 17–18.)

DIAGNOSIS.—Posterior cusp of the row of three minute and indistinct. Anterior cusp of the other row preceded by a slight anterior cingulum which does not form a distinct cusp, and followed by from four to six cusps, the last of which are postero-median in position.

FORMATION AND LOCALITY.—Rhaetic fissure filling, Holwell, near Frome, Somerset.

MATERIAL.—*a*. In the Bath Museum:

M 219. Molar. Holotype. Figd., Owen, 1871, pl. i, fig. 10, as *Microlestes moorei*.

M 221. Molar, so badly worn that reference to this species is very uncertain.

b. In the Yale Peabody Museum:

13622B. Molar, with the largest cusp broken off.

DISCUSSION.—Owen's pl. i, fig. 10, agrees so poorly with the specimen which is marked as the original of it, that only the uniform accuracy of the labels of the Moore Collection at Bath, and the absence of any other specimen which might be the original, convince one that the label is correct. Owen's figure shows three subequal cusps down one side of the tooth, as in *Microcleptes moorei*, while the original appears at first sight to have only two unequal cusps on this side. The third is present but is so minute as to be readily overlooked. The anterior cusp of the other row is lower but stouter than its opposite fellow, and is followed by two cusps

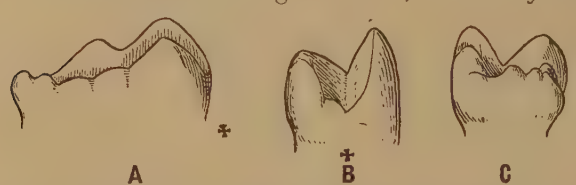


FIG. 17.—*Thomasia anglica* Simpson. Holotype molar. A, side view. B, conventional anterior end. C, conventional posterior end. All × 15 diam. Rhaetic, Holwell, Frome, Somersetshire.

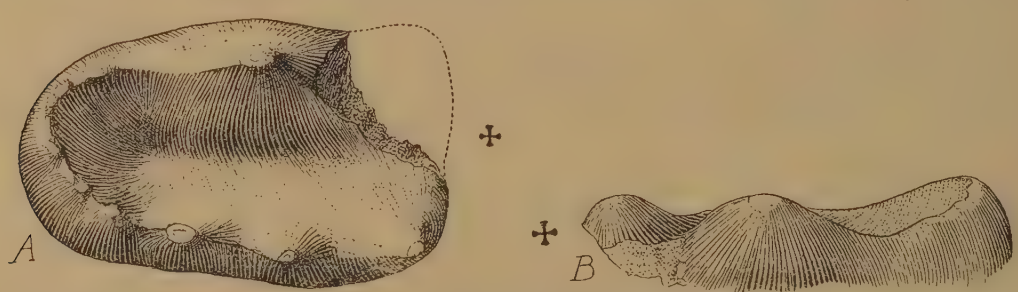


FIG. 18.—*Thomasia anglica* Simpson. Molar, Yale Peabody Museum Cat. No. 13622B. A, crown view. B, side view. × 40 diam. Rhaetic, Holwell, Frome, Somersetshire.

of decreasing size in the same longitudinal series, and then by two more which are somewhat higher, and which are more median in position, forming part of the ridge which closes the basin posteriorly. There is a slight anterior cingulum which shows a tendency to form a cuspule but does not quite do so.

The Yale specimen has lost its largest cusp, but this raises no doubt as to its essential similarity to that of the type, and the rest of the tooth is of great interest. The extremely minute third cusp of the row of three, a character which is believed the most important of the species as opposed to *T. antiqua*, is well shown. At the anterior end of the other row is a cusp about equal in height to the middle one of the row of three, as in the type, and followed by two smaller cusps. The latter are followed by two more, somewhat higher and more median, also as in the type although they are perhaps not quite so distinct. On the ridge between the more median of these and the posterior end of the other row there are, however, two more very minute cusp-like apices which are not seen in the type. The Bath specimen is 1·9 mm. in length and the (broken) Yale specimen 1·55 mm.

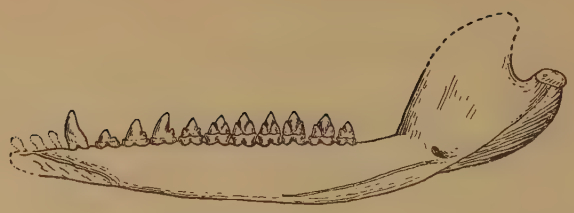
Order TRICONODONTA Osborn.

Diagnosis.—Mammalia having small incisors, three or four in number. Canines present, large. Molars always with three cusps arranged in a longitudinal series; the central cusp of the lower molars usually somewhat higher than the other two, whereas the latter are subequal. Internal cingulum always present. Mandible without angular process, with distinct masseteric and pterygoid crests and high strong coronoid. Zygomata stout, not expanded laterally, arising from posterior ends of alveolar processes of maxillae.

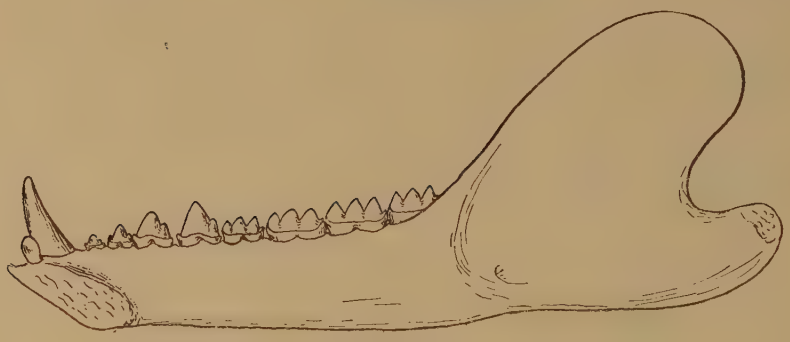
Discussion.—The triconodonts are confined to the Jurassic, where they play a very important part. In the Stonesfield Slate triconodonts make up more than half the known specimens, and in the Purbeck collections, although much less varied and with fewer species than the pantotheres, they are nearly as numerous. In the Morrison fauna, as known, they are less prominent, but still very important.

One of the two original specimens from Stonesfield was a triconodont. Referred at first to *Didelphys* by Broderip (1828, p. 408), it was soon placed by Owen in the genus *Phascolotherium*, the first established genus of triconodonts (Owen, 1839, p. 58). The first Purbeckian triconodont was mentioned in 1859 (Owen, 1859, p. 161).

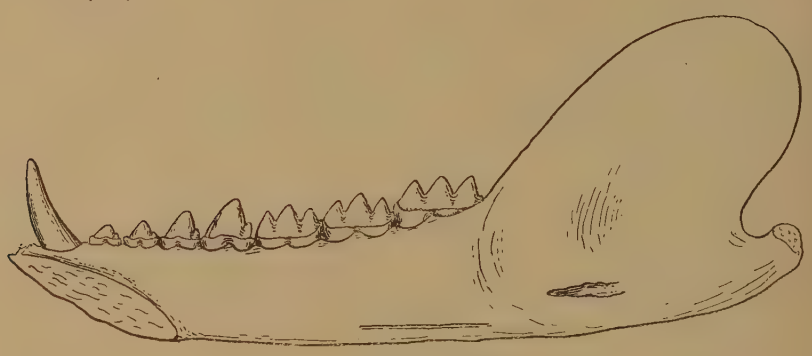
In his memoir (1871) Owen united the then known triconodonts in a so-called typodentate division of marsupials with more than two mandibular incisors, a thoroughly unnatural way of uniting a natural group. Marsh (1887) apparently included the Triconodontidae in the Order Pantotheria, although he does not specifically so state and although his definition of that Order would exclude the triconodonts according to the conceptions of their morphology then held. It was Osborn, however, who crystallized our conceptions of the group as such. In 1888 he referred the Triconodontidae to the Prodidelphia along with his Amphitheriidae, Peralestidae, and Kurtodontidae. This conception was modified, by steps which need not be recapitulated, and his final classification of 1907 recognizes an Order Triconodonta with a single family, Triconodontidae, and four subfamilies—Amphilestinae,



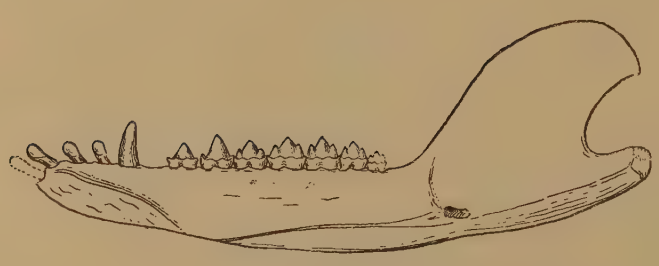
Spalacotherium



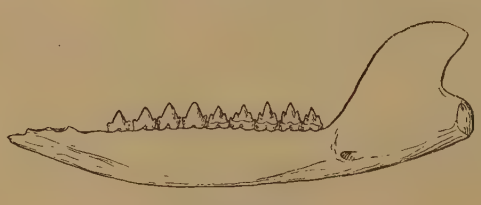
Triconodon



Trioracodon



Phascolotherium



Amphilestes

FIG. 19.—Comparative internal views of right mandibular rami of the European genera of Triconodonta and Symmetrodontá. All × 2½ diam.

Triconodontinae, Phascolotheriinae, and doubtfully also Spalacotheriinae. Subsequent classifications have been largely based on this one, although the subfamily terms are not now in common use.

The most important change which must be made is the removal of *Spalacotherium* and its allies from the Order—a change already suggested (Simpson, 1925D). Examining the three remaining subfamilies, we find that one member of the Phascolotheriinae, *Tinodon*, does not belong to this Order, and that *Phascolotherium* itself does not now appear to present differences of true subfamilial value from *Amphilestes*. Thus only two subfamilies are recognized: the Amphilestinae with the genera *Amphilestes* and *Phascolotherium* from Stonesfield, and *Aploconodon* and *Phascolodon* from the American Morrison; and the Triconodontinae with *Triconodon* from the Purbeckian, *Trioracodon* from the Purbeckian and Morrison, and *Priacodon* from the Morrison.

Evolutionary History of the Triconodonta.

The most primitive triconodont as yet known is undoubtedly *Amphilestes*. It has advanced beyond the reptiles (cynodonts) in the following particulars:

(1) It has symmetrical tricuspid cheek-tooth crowns. Such reptiles as *Cynognathus* and *Microconodon* have similar teeth, although less symmetrical, and it is highly probable that this pattern was inherited from the reptilian ancestry; but in *Amphilestes* the fixity of pattern and the symmetry which is broadly characteristic of the mammalian triconodonts is already established.

(2) Molars and premolars have two separate roots.

(3) The lower jaw has the diagnostic mammalian squamoso-dentary articulation.

The shape of the mandible and condition of the angular region may well have been inherited essentially unchanged from the cynodont stock. Most cynodonts which approach this type have, it is true, a distinct angular process, here lacking, but this is a specialization probably not achieved by the triconodont ancestry. An angular process is not seen in all mammal-like reptiles; it is absent, for example, in *Sesamodon* and in *Dromatherium*.

The dental formula I_4, C_1, P_4, M_5 appears to be primitive for triconodonts. It is the formula of the very primitive *Amphilestes*, and the formulae of all the other known genera could be derived from it by reduction. This formula may also have been inherited from the cynodont ancestors, although it is probable that the latter had two or three more molars than this.

By comparing *Amphilestes* with its Purbeck-Morrison relatives one can gain some conception of what occurred among triconodonts from Middle to Upper Jurassic time. The changes which can be seen to have occurred are as follow:

(1) The premolars became asymmetrical and more sharply differentiated from the molars. The function of the Stonesfield premolars is that of the molars—shearing—whereas the later premolars are more for piercing and grasping.

(2) The anterior and posterior cusps of the molars become relatively larger. This change, which culminates in *Triconodon* with its three equal molar cusps, is

the natural continuation of the conversion of a simple reptilian cone into a complicated cutting device.

(3) Changes occur in the dental formulae. As is usually the case among mammals, these changes are due to reduction. The first change was the loss of the last molar, well under way in *Phascolodon* and *Aploconodon* and complete in all the other Purbeck-Morrison genera. This led from the primitive P_4 M_5 to the P_4 M_4 of *Triconodon*. Reduction followed two lines from this point: another molar may be lost and the remaining ones enlarged, giving the P_4 M_3 of *Trioracodon*, or the anterior premolar may be lost and a postcanine diastema developed, leading to the P_3 M_4 of *Priacodon*. It is not meant that these genera stand in ancestral relationship to each other in the way indicated by their formulae, but only that by comparing them it is possible to see how their characters arose. Even *Amphilestes* shows slight crossing specializations (as the character of the cingulum) which apparently exclude it from the true ancestry of the later stages, yet it certainly gives a valid conception of the structural characteristics of that ancestry.

Nothing is known of the post-Jurassic history of the Triconodonta. It is certain that the group died out before the Tertiary, and probably early in the Cretaceous.

Family TRICONODONTIDAE Marsh.

With the characters of the Order.

Subfamily *AMPHILESTINAE* Osborn.

Diagnosis.—Triconodontidae with premolars symmetrical and submolariform. Molars more than four in number, with the anterior and posterior cusps small relative to the main cusp.

Discussion.—With our present very slight knowledge of the triconodonts it is quite hopeless to attempt to trace any detailed phylogeny within the group. The subfamily Amphilestinae includes four genera which differ among themselves much more than do the three genera of the Triconodontinae. It is probable that these four genera are not indicative of a single phyletic series, or indeed that they are not very closely related, but they are all characterized by the retention of the three characters listed in the definition of the subfamily. All three of these are clearly primitive characters lost in the more highly specialized Triconodontinae. The American Upper Jurassic amphilestines *Phascolodon* and *Aploconodon* do not enter into the present monograph, only the more important and better known *Amphilestes* and *Phascolotherium* being here discussed.

Genus AMPHILESTES Owen.

(Text-fig. 19.)

1845. *Amphitherium* H. v. Meyer (*pars*), Owen, "Odontography," p. 377.

1871. *Amphilestes* Owen, "Fos. Mam. Mesozoic," p. 16.

DIAGNOSIS.—Amphilestinae with dental formula, $I_{3\ or\ 4}$, C_1, P_4, M_5. Molar cusps high and slender. Molar cingulum rising below the median cusp. Molar enamel not pitted.

GENOTYPE.—*Amphitherium broderipii* Owen.

Amphilestes broderipii (Owen).

(Text-figs. 20–21.)

1845. *Amphitherium broderipii* Owen, "Odontography," p. 377.

1887. *Amphilestes broderipii* Lydekker, "Cat. Fos. Mam. B.M. (N.H.)," V, p. 271.

See also, Owen, 1871, p. 17; Osborn, 1888A, p. 193, 1888B, p. 292; Goodrich, 1894, p. 14.

DIAGNOSIS.—(The only species of the genus.)

FORMATION AND LOCALITY.—Stonesfield Slate at Stonesfield, Oxfordshire.

MATERIAL.—*a*. In the Yorkshire Museum:

Left ramus, internal aspect, with P_{1-3} and M_{1-5}. Holotype. Figd., Owen, 1871, pl. i, fig. 25; Osborn, 1888A, pl. viii, fig. 1; Goodrich, 1894, pl. xxvi., fig. 5; and elsewhere.

b. In the University Museum, Oxford:

I. Left ramus in external aspect with P_{2-4} and M_{1-5}. For descriptive purposes this may be spoken of as the first Oxford specimen. Figd., Goodrich, 1894, pl. xxvi, fig. 6.

II. Right ramus, external aspect, with P_{2-4} and M_{1-5}. This may be known as the second Oxford specimen. Figd., Goodrich, 1894, pl. xxvi, fig. 7.

c. In the British Museum:

M 2297. Cast of the first Oxford specimen. (*Presented by Prof. Prestwich*, 1885.)

DENTITION.

DENTAL FORMULA.—Owen (1871, p. 15) considered this form to have the cheek-tooth formula P_6, M_6. Lydekker (1887, p. 271) suggested that P_4, M_7 might represent the true formula, and this was at first accepted by Osborn (1888A, p. 193). Later, however, Osborn (1888B, p. 293) gives P_4, M_6. Goodrich (1894, p. 16) justly criticizes this conclusion and gives P_4, M_5. The latter formula certainly must be adopted. The type has three premolars, then a space for one tooth, then five molars. If the missing tooth is a molar the formula would be $P_{3\ or\ 4}$, M_6, while if a premolar it would be P_4, M_5. The first Oxford specimen settles the question, as it shows five molars, preceded by three premolars and alveoli for another. There are also seen an elongated canine alveolus and three incisive alveoli. A fourth incisive alveolus may have been present more anteriorly, where the jaw is slightly broken, so that the entire formula is $I_{3\ or\ 4}$, C_1, P_4, M_5.

INCISORS.—A single, nearly erect, columnar posterior incisor is preserved in

the type. The peculiar short pointed projections believed by Goodrich to be the remains of incisors in the first Oxford specimen prove to be only the plates of bone between the alveoli. The actual incisors are missing in this specimen.

CANINE.—The canine is missing, but, from the alveoli, it was apparently large and two-rooted.

PREMOLARS.—The premolars increase in size from P_1 to P_4, and the latter is higher than M_1 but about the same height as M_{3-4}. The premolars are quite different from the molars in pattern and the difference in degree of protrusion is equally marked. The old belief that in this form (or in any Stonesfield mammal) the premolars and molars were not well differentiated is entirely false. The premolars have a high, laterally compressed, trenchant and piercing main cusp and single anterior and posterior accessory cusps of small size (intermediate in size and in relative position on the crown between the accessory cusps and the cingulum cusps of the true molars). There are no cingula, external or internal. The premolars are very nearly symmetrical.

MOLARS.—The five molars are similar save in size. M_{3-4} are the largest and

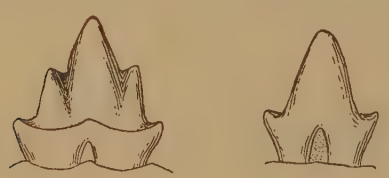


FIG. 20.—*Amphilestes broderipii* (Owen). A, M_3, internal aspect. B, P_1, internal aspect. Drawn from holotype, × 15 diam. Middle Jurassic, Stonesfield Slate, Stonesfield, Oxfordshire.

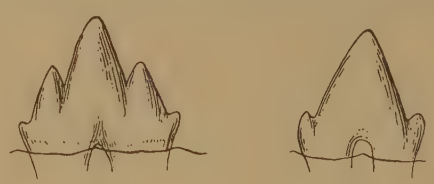


FIG. 21.—*Amphilestes broderipii* (Owen). A, M_3, external aspect. B, P_1, external aspect. Drawn from Oxford I, × 15 diam. Same origin as holotype.

are of about equal size; the others are progressively smaller. The cusps are more slender and at the same time less compressed transversely than in *Phascolotherium*. The central cusp, at least, appears to be about as broad as long. Anterior and posterior to this central cusp are smaller accessory cusps and below these are very small anterior and posterior cingulum cusps. These pass into the internal cingulum, which is continuous and rises once, on the central cusp. There is no external cingulum, and this face of the tooth is quite strongly convex, with smooth enamel.

MANDIBLE.

The lower jaw is of the almost invariable triconodont type. The alveolar border is more or less straight, while the lower border forms a single gently convex curve from the condyle to the symphysis. The dental foramen is at the anterior end of the very shallow pterygoid fossa. The angular region is not well shown, but certainly was, as in other triconodonts, without any true angle but with a low, sharp pterygoid crest running back to the condyle. The posterior mental foramen is far back, beneath the posterior root of M_1; there appear to be others beneath the anterior root of P_3, beneath P_2, and perhaps others in front of this.

MEASUREMENTS.

	P_1.	P_2.	P_3.	P_4.	P_{2-4}.	M_1.	M_2.	M_3.	M_4.	M_5.	M_{1-5}.	P_2–M_5.	Depth below M_3 outside.
York ..	1·1	1·1	*ca.*1·1	*ca.*1·2	*ca.*4·0	*ca.*1·5	1·6	1·6	1·5	1·4	6·8	—	—
Oxford I ..	—	1·0	1·2	1·2	3·5	1·4	1·5	1·6	1·5	1·3	7·3	10·7	2·3
Oxford II ..	—	1·0	1·1	1·2	3·8	1·4	1·5	1·5	1·4	1·3	6·9	10·8	2·3

GENUS PHASCOLOTHERIUM Owen.

(Text-fig. 19.)

1838. *Phascolotherium* Owen, *Proc. Geol. Soc.*, III, p. 9.

DIAGNOSIS.—Amphilestinae with dental formula $I_4 . C_1 . P_2 . M_5$. Molar cusps longer, less slender, more compressed. Internal cingulum rising slightly at two places, just anterior and posterior to the main cusp. Molar enamel pitted or finely rugose.

GENOTYPE.—*P. bucklandi* Broderip.

Phascolotherium bucklandi (Broderip).

(Pl. IV, fig. 1 ; Text-figs. 22–23.)

1828. *Didelphys bucklandi* Broderip, *Zool. Jour.*, III, p. 408.

1838. *Thylacotherium bucklandi* Valenciennes, *C. R. Acad. Sci.*, Paris, VII, p. 580.

1841. *Phascolotherium bucklandi* Owen, *Trans. Geol. Soc.*, p. 58.

See also Owen, 1871, p. 16 ; Lydekker, 1887, p. 270 ; Osborn, 1888A, p. 194, 1888B, p. 293 ; Goodrich, 1894, p. 11.

DIAGNOSIS.—The only species of the genus.

FORMATION AND LOCALITY.—Stonesfield Slate at Stonesfield, Oxfordshire.

MATERIAL.—*a*. In the British Museum :

112. Right ramus, internal aspect, nearly complete, with I_{2-4}, C, P_{1-2} and M_{1-4}. Holotype and one of the two original specimens brought to light by Broderip in 1812 or 1814. Figd., Broderip, 1828, pl. xl ; Buckland, 1836, pl. ii ; de Blainville, 1838 ; Owen, 1842, pl. vi, fig. 2, and 1871, pl. i, fig. 26 ; Osborn, 1888A, pl. viii, fig. 3 ; and elsewhere. (*Presented by W. J. Broderip, Esq. No date.*)

M 2300. Cast of the Oxford Specimen. (*Presented by Prof. Prestwich*, 1885.)

M 7595. Right ramus, internal aspect with P_2 and M_{1-4}. This specimen has never been mentioned or figured. (*G. H. Morton Collection. Purchased* 1900.)

b. In the University Museum, Oxford :

I. Left ramus, internal aspect, with I_2 and four molars. Figd., Goodrich, 1894, pl. xxvi, fig. 8.

II. Model, enlarged six times, of the posterior part of a right ramus. The original contained three molars and was seen in internal view. This

was Parker's specimen, mentioned by Osborn (1888B) and described and figured Goodrich (1894, pl. xxvi, fig. 9). The model was prepared by Prof. Sollas by his method of serial grinding, the original being destroyed.

Dentition.

Dental Formula.—The dental formula of the type is not in doubt. It is $I_4 . C_1 . P_2 . M_5$. The first incisor is missing, but its alveolus is seen. The last molar apparently was present. It is shown in all the older figures, but now only its roots remain. Owen believed the cheek series of this animal not to be divisible into premolars and molars, and Osborn at first accepted this, but later was the first to point out the morphological break between the second and third cheek teeth (1888B, p. 294). Goodrich (1894, p. 13) also emphasized this point. We may add that the difference involves not only cusp proportions, as pointed out by Osborn, but also the actual tooth structure. The same thing is shown, perhaps most clearly in the hitherto unstudied M 7595, by the marked break with regard to degree of protrusion.

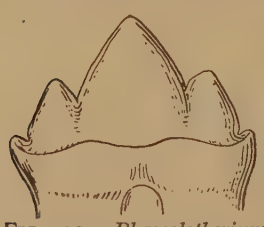


Fig. 22.—*Phascolotherium bucklandi* (Broderip). Internal aspect of left M_2, Oxford specimen. × 15 diam. Middle Jurassic, Stonesfield Slate, Stonesfield, Oxfordshire.

Remarkable as it is, there can be no doubt that *Phascolotherium* had but two premolars. The holotype had five molars in use. M 7595 has four molars only, but there appears to be a definite germ of the fifth still in its formative capsule beneath the anterior end of the coronoid. In the Oxford specimen there are four molars preserved and Goodrich believed there were alveoli for the first, anterior to them. From the measurements, however, it seems more probable that these are M_{1-4} and that M_5 had not yet come into use. In both 112 and M 7595 M_4 is exactly the size of the last tooth of the Oxford specimen, while M_5 is much smaller. The last tooth in the Parker specimen as figured was probably also M_4. The conditions as regard tooth growth would seem to have been much the same in *Phascolotherium* as in *Triconodon*, the last molar coming into use late in life. In *Phascolotherium*, as in the later *Phascolodon* and *Aploconodon*, this tooth seems to have been in process of reduction or loss.

Incisors.—I_{2-4} are similar, stout teeth, not sharply pointed but with subspatulate tips. They are all of about the same size, and are separated by spaces slightly less than the antero-posterior diameter of their crowns. They are in a nearly longitudinal series.

Canine.—The canine is not greatly enlarged. It is somewhat more erect and stouter than the incisors, with its apex slightly recurved. There appears to have been only one root.

Premolars.—Both premolars are present in the type and the second is present in M 7595. The first is slightly smaller than the second, the latter being about as tall as M_1. In the holotype M_1 is worn, so that it is shorter than the premolar; in M 7595 the premolar is shorter because it is not fully protruded. As pointed out by Osborn, the main cusp of the premolar is taller and more slender relatively

than that of the molars. A further difference seems to be in the presence of only three cusps in the premolars, whereas the molars have five. As in *Amphilestes*, the single pair of premolar accessory cusps is of a size between that of the accessory cusps and of the cingulum cusps on the molars. The premolars have an internal cingulum (the external face is unknown) and, as does the molar cingulum of this genus, it curves upwards twice in traversing the inner face of the tooth.

Molars.—M_{2-3} are the largest, the others progressively smaller. With the possible exception of M_5, which is no longer shown by any specimen and which is not clearly portrayed in the older figures, all the molars are of the same structure. They are similar to those of *Amphilestes*, having a high central cusp, lower anterior and posterior accessory cusps, and small anterior and posterior cusps which terminate the sharp and continuous internal cingulum. The whole tooth, however, is lower and longer than the corresponding one of *Amphilestes*, and relatively more compressed transversely. The cingulum, instead of rising below the main cusp, curves gently upwards in two places, just anterior and posterior to the central cusp. They do not, as shown in some figures, rise to sharp points, nor is this feature perfectly regular.

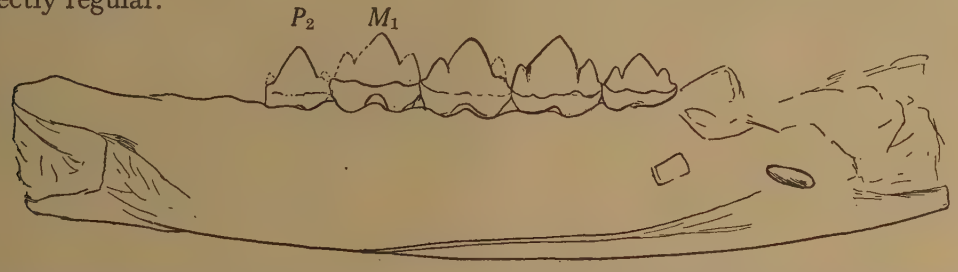


Fig. 23.—*Phascolotherium bucklandi* (Broderip). Internal aspect of right mandibular ramus, B.M. No. M 7595. × 6 diam. Middle Jurassic, Stonesfield Slate, Stonesfield, Oxfordshire.

All students of this genus have commented on the fine pitting of the enamel. It is present in all specimens, and is certainly an original feature of the teeth. It does not extend below the cingulum internally.

In his work on this genus Osborn placed considerable emphasis on his observation that in the molars " the lateral cusps project partly from the inner slopes of the main cusp and are not precisely in line " (1888A, p. 195). This view became a vital link in Osborn's restatement and support of Cope's derivation of the tritubercular molar from the triconodont one, and it was also believed to permit the placing of *Phascolotherium* and *Tinodon* in the same subfamily. (See Osborn, 1888A, pp. 229, 243, 251 ; 1907, p. 22). This conclusion is of the greatest importance and demands reconsideration in view of the better optical instruments and fuller series of comparative material now available. Goodrich (1894, p. 21) has already stated that he could find no trace in *Phascolotherium* of the supposed relative outward movement of the main cusp. Except for the destroyed Parker specimen all the known material, including a specimen not previously studied, has been thoroughly studied with a binocular microscope, an instrument not available either to Osborn or Goodrich. The result fully confirms the work of Professor Goodrich. There appears to be no

support whatever for the view that the accessory cusps of the molars are more internal than in the other triconodonts.

Mandible.

The nearly straight alveolar border, curving upward somewhat in the incisive region; the sweeping curve of the lower border from condyle to symphysis; the long cartilaginous symphysial union extending back to a point beneath the post-canine diastema; all these are typical of the Triconodonta generally. As is usually the case, the pterygoid crest is broken in the specimens which show it, so that it gives the impression of being the attachment for a thin and highly inflected angular process. This is not so. There is no angular process in the Triconodonta and the pterygoid crest is a low but sharp continuous ridge from the articular condyle to below the dental foramen. The masseteric crest, best shown by the Sollas model of the Parker specimen, is developed into a fairly wide efflected flange, even more prominent in some of the Upper Jurassic forms. The internal groove has the peculiarity, shared by all the specimens which show it in its entirety (112, M 7595, and Oxford), of descending to the lower border before reaching the symphysis and proceeding, rather indefinitely, along the inferior face of the ramus. This is most marked in M 7595. Another peculiarity, recalling the Morrison *Trioracodon bisulcus*, is seen in 112, where the groove is distinctly branched just before reaching the dental foramen posteriorly.

The articular surface of the condyle is oval, with its longer axis transverse. The coronoid process is high and broad, and has a characteristic shape well shown in the figure.

Measurements.

	P_2.	M_1.	M_2.	M_3.	M_4.	Depth below M_3 inside.	Post. end M_4 to condyle.
112,, ...	1·6	2·0	2·25	2·2	1·8	4·7	14·5
M 7595	1·5	2·1	2·2	2·1	1·8	3·6	—
Oxford	—	2·1	2·3	2·1	1·8	4·0	11·6
Parker	—	—	—	—	—	5·0	14·5

The two measurements of the Parker specimen are taken from Prof. Goodrich's figure, but are probably quite accurate. The great variation in size of jaw is certainly due largely or wholly to age. M 7595 is the youngest specimen, as evidenced not only by its slender ramus but also by the incomplete protrusion of P_2 and inclusion of M_2 wholly within the base of the coronoid. The Oxford specimen is somewhat older, whereas the type, 112, is fully adult, with the entire tooth series in use, molars somewhat worn, stout ramus, and large coronoid. The Parker specimen was also apparently fully adult. If the original were still available one would expect to find alveoli for the small M_5 behind the teeth that were preserved.

Subfamily *TRICONODONTINAE* Osborn.

Triconodontidae with premolars asymmetrical, more or less recurved, the last ones higher than the first molars. Molars four or three in number, with anterior and posterior cusps nearly or quite equal to the mid-cusp.

Genus TRICONODON Owen.

(Text-fig. 19.)

1859. *Triconodon* Owen, *Encyc. Britannica*, 8th ed., XVII, p. 161.

1871. *Triacanthodon* Owen, " Fos. Mam. Mesozoic," p. 72.

1874. *Galestes* Gore, " Glossary Foss. Mam.," p. 22. (*Nom. nud.*)

Diagnosis.—Triconodontinae with dental formula : $I^{\frac{1}{1}}_{\frac{1}{1}}$ $C^{\frac{1}{1}}_{1}$ $P^{\frac{3}{3}}_{4}$ $M^{\frac{4}{4}}_{4}$. Anterior and posterior cusps of lower molars usually quite as high as the midcusp. M^3 not reduced. M^4 reduced but still retaining the three original columnar cusps.

Genotype.—*T. mordax* Owen.

All the Purbeckian forms and one from the Morrison have been referred to this genus, but it now appears that only the genotype belongs here, all the other valid species being very definitely distinct generically.

Triconodon mordax Owen.

(Pl. IV, figs. 2–5 ; Pl. V, figs. 1–5 ; Text-figs. 24–26, 30*c*.)

1859. *Triconodon mordax* Owen, *Encyc. Britannica*, 8th ed., XVII, p. 161.

1871. *Triconodon minor* Owen, " Fos. Mam. Mesozoic," pl. iv, fig. 6.

1871. *Triacanthodon serrula* Owen, " Fos. Mam. Mesozoic," p. 72.

See also Owen, 1860, p. 318, 1871, p. 58 ; Lydekker, 1887, p. 258 ; Osborn, 1888A, p. 195.

Diagnosis.—The only species of the genus. Length M_{1-3} about 8 mm.

Formation and Locality.—Middle Purbeckian, Durdlestone Bay, Swanage, Dorset.

Material.—(*a*) In the British Museum. (*All, except two casts, from Beckles Colln., purchased* 1876.)

47764. Left mandibular ramus, nearly complete, seen in external aspect, with crowns of C, P_2, P_4 and M_{1-3}. Holotype. Figd., Owen, 1859, fig. 86, 1871, pl. iii, fig. 7.

47763. Two slabs of matrix. A, with the posterior end of the left mandibular ramus with the unerupted M_4, in internal aspect, the right parietal and natural internal cast of the left, the basisphenoid, a small piece of the lateral portion of the left frontal, and some unidentifiable fragments. B, with the anterior part of the left mandibular ramus with I_4, dc, C, P_{1-4}, dm_4, M_{1-2}, in external aspect, most of the right frontal, right and left periotics, the atlas, a limb bone, and unidentifiable fragments. This is the holotype of *Triacanthodon serrula* and the lower jaw (but nothing else) is figured. Owen 1871, pl. iv, figs. 7–8 ; Osborn 1888, pl. viii, fig. 5 ; Thomas 1887, pl. xxvii, fig. 10.

47767. Broken right mandibular ramus with P_1, P_4 and M_1 in external aspect. Figd., Owen, 1871, pl. iii, fig. 10.

47768. Broken right ramus with P_4 and parts of P_3 and M_{1-2}. Outer aspect. Figd., Owen, 1871, pl. iii, fig. 15.

47771. Broken right ramus with M_{1-3}. Internal aspect. Holotype of *Triconodon minor*. Figd., Owen, 1871, pl. iv, fig. 6.

47784. Part of right maxilla with M^{2-3}. Figd., Owen, 1871, pl. iv, fig. 5.

47789. Matrix impression of internal aspect of right ramus with P_4 and M_{1-3}.

47790. Matrix impression of external aspect of left ramus with P_4 and M_{1-3}.

47793*a*. Fragment of left ramus with M_3, external aspect.

47794. Fragment of right ramus with two broken premolars. External aspect.

47796. Part of right maxilla with M^{3-4}.

47806. Part of right maxilla with two molars.

48395. Part of right mandibular ramus with C, P_{3-4}, and M_{1-4}, internal aspect, and associated right ramus with P_4 and M_{1-3}, external aspect, and isolated right canine.

48396. Part of right maxilla with M^{3-4} in outer aspect.

M 79. Cast of the specimen in the Museum of Practical Geology. (*Presented by H. Willett, Esq.*, 1881.)

M 3705. Cast of same specimen before complete development. (*Made in the Museum.*)

(*b*) In the Museum of Practical Geology, London.

Right mandibular ramus with P_{3-4} and M_{1-4} in external aspect. Figd., Willett, 1881, text-figure. (*Presented by H. Willett, Esq.*)

This is one of the most abundant and best-known species of Jurassic mammals. In taking it to be the genotype we disagree with Osborn, who speaks of "*T. ferox*, which has been selected as the type in this memoir." The matter, however, does not seem to be one for selection: *T. mordax* was established in 1859 and always served Owen as the basis of the genus. *T. ferox* was not established until 1871. This acceptance of Owen's genotype is more important now than when Osborn wrote, as the two species prove to belong to different genera.

Lower Dentition.

Dental Formula.—No known specimen shows the number of incisors. In 47763 one incisor is preserved and there is at least one more incisive alveolus. The original number was probably three or four. The canine is, of course, always present, and the premolars are clearly four in number. It was the belief of Owen (1871) and it was also, by analogy with the American forms, my earlier view (Simpson, 1925A, pp. 153–4), that *Triconodon mordax* was characterized by the possession of only three molars. Lydekker (1887, p. 258) suggested that this species had four molars and was in fact synonymous with *Triacanthodon serrula*, the last molar coming into use late in life. This idea was accepted and elaborated by Osborn (1888A, pp. 197–9). The view of Lydekker and Osborn now proves to be correct, and that of Owen and myself wrong.

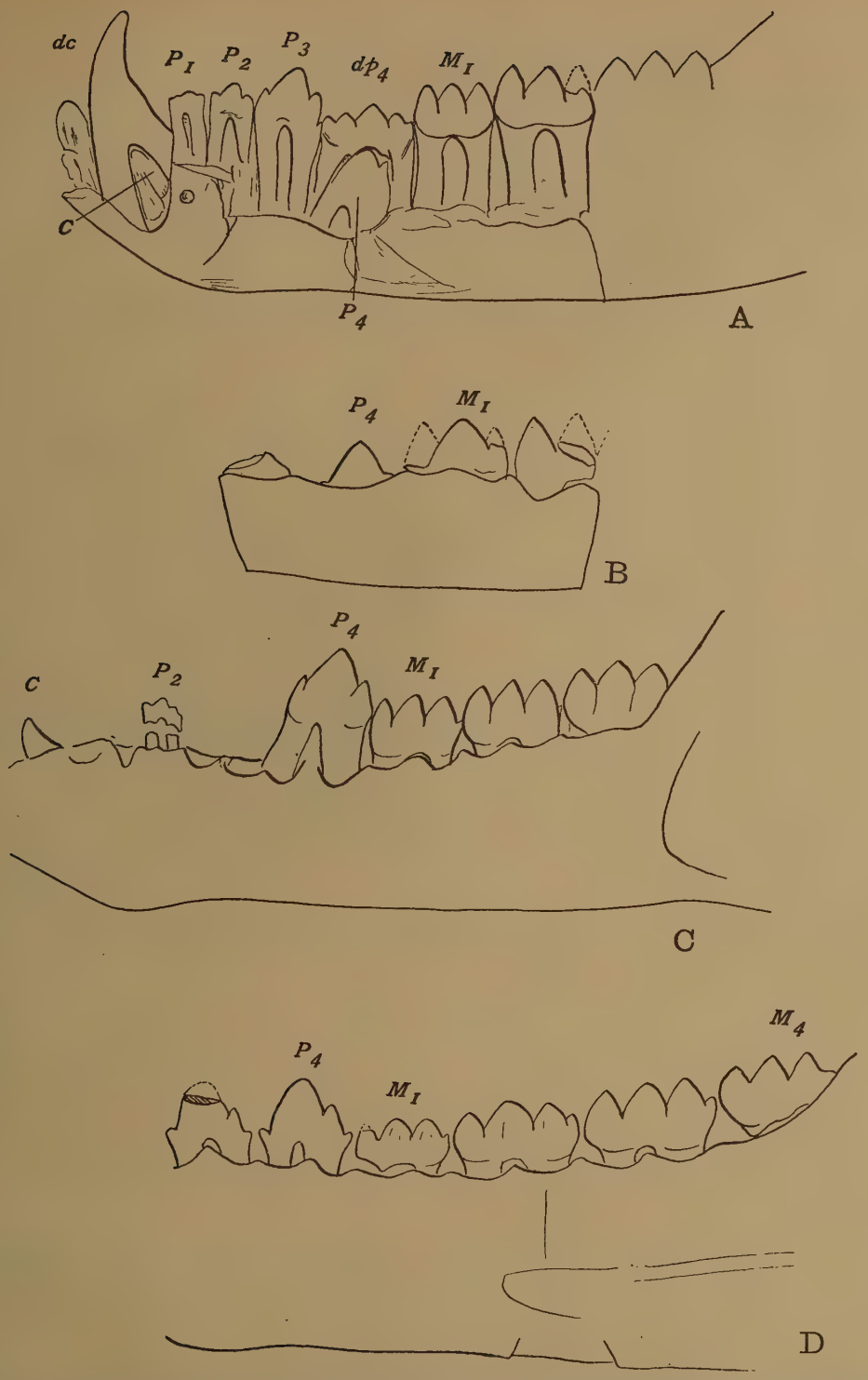


FIG. 24.—*Triconodon mordax* Owen. Series of external views of left mandibular rami, to show tooth replacement. A, B.M. 47763, with deciduous canine and dp_4. B, B.M. 47768, with P_4 just coming into use. C, B.M. 47764, with P_4 fully emergent, C coming into use, but M_4 still in the formative capsule. D, Willett's specimen, an aged individual with all permanent teeth in use. All × 6 diam.

There are six specimens of this genus in which the number of molars present can be counted with some certainty :

(*a*) Three molars visible : 47764.

(*b*) Three molars in use, but a fourth visible in its formative capsule : 47763.

(*c*) M_4 just coming into use : 47767, 47771, 48395.

(*d*) M_4 fully functional : Willett's specimen (Mus. Pract. Geol.).

Thus of the specimens in which the molar number can be ascertained, five certainly have four molars. The other differs in no other respect and it seems a certain conclusion that it also has a fourth molar still concealed in the unbroken formative capsule.

No specimen of the upper jaw permits a certain count of the molars, although from the alveoli, and from comparisons with the lower jaws and with *Trioracodon*, there can be no question that it also had four. The formula as now known may therefore be written as follows : $I^1_1 . C^1_1 . P^1_4 . M^4_4$.

Tooth Replacement.—Owen (1871, p. 73) suggested that the fourth cheek tooth of 47763 might be the last deciduous molar, and Osborn (1888, p. 198) accepted this view. Thomas (1887, p. 443) dissected the side wall of the mandible of this specimen and revealed the presence of the true P_4 beneath the tooth now definitely proved to be dm_4. He believed this to be the only tooth changed and to indicate that the marsupial type of tooth succession is primitive.

Restudy of Thomas's dissection, however, shows that he overlooked a very important point : the canine also has a permanent successor below it. Thus we know that C and P_4 had deciduous predecessors, and we do not know that the incisors and P_{1-3} did not also have predecessors, for at this stage they would in any event have been already replaced. In view of the unworn nature of P_{1-3} and the obvious fact that they belong to quite a different dentition from dm_4 and to the same dentition as P_4, it seems probable that, as would be expected, the tooth change in this jaw was as complete as in primitive placentals, or as in the cynodonts. The later stages of the development of the lower jaw may be made out from various specimens :

1. Hypothetical stage with deciduous incisors, canine, and dm_{1-4}. Not represented by any specimen.

2. Permanent incisors, deciduous canine, P_{1-3}, dm_4, and the first three permanent molars in use. 47763.

3. Dm_4 shed and P_4 just coming into use. 47768.

4. *Dc* shed and C just coming into use. P_4 fully emerged, only three permanent molars in use. 47764.

5. Tooth replacement complete and all four molars in use. Willett's specimen.

Tooth replacement in this species seems to have been rather slower than in most Mesozoic mammals, although the fact that so many more growth-stages are known here than in the other forms may be accidental.

Incisors.—47763 is the only specimen which shows an incisor of this species. In it the lateral incisor is shown. It is a small tooth with a rounded subspatulate tip, the outer aspect of which bears two slight longitudinal depressions. The incisors

appear to have been arranged in a transverse arc rather than in an almost straight longitudinal series.

CANINE.—The deciduous canine is seen in 47763. It is a large, sharply pointed, recurved tooth with two stout divergent roots, the anterior somewhat larger and more external. Between these roots is seen the permanent canine, but its form cannot be made out. On 48395 both permanent canines are seen. The apices are like that of the deciduous tooth, fairly sharp and recurved, but the teeth appear to have been implanted by a single fang.

PREMOLARS.—The four premolars are of similar structure, but they differ in size and proportions, becoming larger and relatively higher from P_1 to P_4. Each consists of a high, trenchant, laterally compressed central cusp with a small posterior accessory cusp, below which is a minute posterior cingulum cusp; there is an anterior cingulum cusp intermediate in size and in height between the posterior accessory and posterior cingulum cusps. There is no external cingulum, but, at least on P_{3-4}, there is a sharp continuous internal cingulum, rising slightly below the central cusp. P_4 is somewhat higher than the following molars.

DECIDUOUS MOLARS.—Only dm_4 is known. Its degree of protrusion clearly shows that it is not a member of the same series as the preceding (permanent) premolars in the same specimen (47763), but that it is closer to what would be expected of a true molar in this position. In form also it resembles a molar rather than a premolar, but it is quite distinct from the true molars. The crown is long and depressed, with a low blunt main cusp somewhat posterior to the centre of the tooth, with slightly smaller anterior and posterior accessory cusps, and very small anterior and posterior cingulum cusps, the anterior a little the larger of the two. It thus has five distinct cusps. Its roots are very widely divergent and P_4 may be seen between them.

MOLARS.—The molars increase in size from M_1 to M_3, while M_4 is very slightly smaller than the preceding tooth. Each has three main cusps following each other in a straight longitudinal series. The cusps are laterally compressed and trenchant, the external face convex, the internal convex centrally, but concave near the cutting edges. The cusps in most specimens are neither so slender nor so sharply pointed as in the other genera of the subfamily. The three cusps are nearly equal, although the first tends to be very slightly smaller than the other two, and all point a little backward. There is a sharp, continuous, faintly nodulated, internal cingulum which passes into a small but definite posterior cingulum cusp on each tooth directly behind the third main cusp. Although always present, this cusp is easily overlooked as it fits into a vertical groove in the anterior face of the succeeding tooth and is also generally hidden by the matrix.

The molars of 48395 have cusps which are somewhat more slender and more sharply pointed than those of the holotype, but this may well be due to wear, the individual being an older one. Wear in this group does not necessarily blunt the lower molar cusps but tends rather to keep them sharpened. The teeth are also a little smaller than those of the holotype, but they are within the range of the group.

47771 was made the holotype of a new species, *T. minor*, by Owen on the basis

of the molar structure. The inclination backward of the cusps and the posterior basal prominence are equally characteristic of *T. mordax*, and the specimen is not sufficiently well preserved to warrant assigning any value to the apparent absence of crenulations in the molar cingula.

Lower Jaw.

The lower jaw of *Triconodon* is that of a powerful, though diminutive, carnivore. The rounded coronoid process is high and broad and is separated from the condyle by a notch of moderate depth. The condyle was not borne on a definite constricted neck. The shape of the articular surface cannot be made out on any specimen of this genus, but no doubt was much as in *Trioracodon*. The masseteric fossa is well developed, clearly defined anteriorly and bounded inferiorly by the prominent efflected masseteric crest. The character of the pterygoid fossa and crest was apparently much as in *Trioracodon*, where it is much better known.

The symphysial surface extends back to beneath the posterior end of P_2. Owen laid stress on the way in which the symphysis appeared to him to rise abruptly from the lower border, but comparison with specimens of which this is not true seems to indicate that the difference is not in the character of the symphysis but in the greater or less development of a slight swelling in the lower border beneath P_1. This apparently helped to lodge the long canine roots and becomes less marked in older specimens when the canine is fully protruded.

The mental foramina were apparently rather variable. From Owen's figure and description we learn that 47763 originally had a mental foramen beneath the posterior end of the canine and two more successively smaller ones beneath P_1 and P_2 respectively. In 47764, on the contrary, there is but one mental foramen, beneath P_1.

Upper Dentition.

There are only four specimens of upper jaws referable to this species in the collections and they reveal only M^{2-4}. The positive statement that there were four upper molars is based on knowledge of triconodont occlusion generally, and especially on the conditions in the related species *Trioracodon ferox*, which indicate that a functional lower M_4, like that of *Triconodon mordax* in which this tooth is almost as large as M_3, would require a large and functional M^4 above.

Two molars which are taken to be M^{2-3} of the right side are seen in 47806. As already pointed out at length elsewhere (Simpson 1925A), the triconodont upper molars are by no means simply reversed lowers but have a different function and morphology. Above the somewhat swollen outer base and separated from it by the external cingulum is the relatively flat sloping outer surface of the crown. Although this surface rises to the three apices of the tooth, there is no definite division into three convexities corresponding to the cusps. The external cingulum is sharp and continuous, but somewhat irregular on this specimen. It rises to a tiny antero-external cuspule, then passes in a broad curve to the posterior end of the tooth, where it rises into a small posterior cusp behind the three main cusps. Internally

the cusps are well differentiated, with a columnar aspect, separated by valleys up which the lower molar cusps scraped. Although the teeth on this specimen are almost unworn, the internal cingula are very faint, rounded, and discontinuous, forming no internal cusps. M^3 is somewhat larger than M^2, but there are no noteworthy morphological differences between them.

In 48396 M^{3-4} are preserved. M^3 agrees well enough with that of the specimen just described. The outer base is less gibbous, the cingulum more regular, and the small posterior column is almost lacking, but these minor differences are probably within the range of variation of the species. M^4 is of very great interest and importance, especially when it is contrasted with the last upper molar (M^3) of *Trioracodon*. It is just coming into use and is unworn. It is somewhat smaller than the preceding teeth and is narrower posteriorly instead of being nearly equal in width throughout. The three main columns or cusps of each of the preceding molars are seen here also. Only the first is of full size, the others decreasing rapidly in prominence. A small fourth column also occurs. Apparently there is an external cingulum, but the wall of the alveolus hides most of it. There appears to be a slight cingular shelf internal to the first and third cusps, but not to the second.

47784 includes a broken M^2 and complete M^3. The teeth are slightly larger than those of the preceding two specimens and are more worn. The outer bases are more swollen than in 48396 and the cingula are more regular than in 47806, but it may be referred to the same species. The alveoli for M^4 are seen.

Skull.

The maxilla of *Triconodon* is best shown in 47784, although even here it is very imperfect. It closely resembles the same element in *Trioracodon* (see below). Below the orbit it is a simple and rather slender bar of bone containing the molar roots. Posteriorly it continues straight backwards and somewhat upwards, tapering to a point, and no doubt articulating with the jugal, which is not preserved. Outside the last molar it sends downward a short pointed process which partly conceals this tooth from view when seen from the external aspect. Between this process and that which passes into the zygoma the bone is distinctly excavated for the origin of the anterior part of the masseter. The palate is poorly preserved, but it is clear that there is a posterior lateral emargination, as already shown in the American *Priacodon* (Simpson 1925A, fig. 16), extending forward to the anterior end of M^4 in this case.

Our only other knowledge of the skull of *Triconodon* comes from the two slabs included under 47763. On these several scattered cranial elements are seen in association with a lower jaw referable to this species. That this association is not accidental but indicates the derivation of the bones in question from a single animal seems assured. All the bones are clearly mammalian, the size relationships are correct, no parts are duplicated, and in another specimen (47797) a frontal bone differing in no important respect from that here preserved is seen in direct association with a triconodont upper dentition.

As seen by the incomplete replacement of the lower teeth, the individual was young and the cranial elements became separated along the sutures. Parietals,

a frontal, basisphenoid and part of an alisphenoid, both periotics, the axis, a limb bone, and some unidentifiable fragments are seen.

The left parietal is chiefly represented by its internal cast, and the right is seen in external aspect. The two bones appear to have been fused along the midline posteriorly, but still to be separate anteriorly. They are long bones, narrowing slightly anteriorly. The body of the bone is thin and plate-like and, apparently, was closely applied to the enveloping membranes of the brain, although the superficial blood-vessels have left no impress on the internal surface. As best seen in the natural external mould of the counterpart slab, there is a sharp sagittal crest beginning at the anterior end of the parietals and becoming narrower and higher posteriorly. At the posterior end this crest bifurcates and passes into the lambdoid crests, but the latter were apparently not well developed. As seen from above, the posterior contour of the parietals, here fused, is indented in the mid-line. The sutural surface for the supra-occipital is wide, measuring about 2 mm. antero-posteriorly, and faces almost directly downward but a little backward.

The left frontal only is preserved, being seen on one slab in the internal aspect of the dorsal portion, on the other in a section of the lateral portion. This bone was not fused with the corresponding one on the opposite side. Like the parietal it is long and of nearly the same width throughout. There is a definite but slight post-orbital constriction just posterior to the olfactory lobes.

The cranium must have been elongated and tubular after the fashion characteristic of the recent insectivores. It must have been quite close to the skull of *Gymnura* in general aspect.

The rather fragmentary and crushed nature of the specimen does not allow much precision of detail in this respect, but there clearly was some development of frontal sinuses in the roof of the anterior part of the cerebral hemispheres and in the region between these and the olfactory lobes.

In keeping with the tubular character of the skull, the posterior part of the nasal cavity is about as wide as any part of the brain-case.

From the parts preserved the frontal plus parietal length cannot have been less than 27 mm. and was probably slightly greater. The length of the lower jaw associated with this material is not over 28·5 mm. The occiput must have been either vertical or inclined slightly forward, and we may reasonably assume, from the nature of the dentition, that the anterior end of the lower jaw was within a millimetre or so of the anterior end of the skull, and perhaps even in advance of the tips of the nasals. It follows that the distance between the glenoid fossa and the occiput must have been relatively large. It was apparently as much as one-fourth of the total length of the skull, perhaps even more. This fact is of great interest and importance, for it indicates that the specialization of the basicranial structure was proceeding on lines quite different from those seen in the monotremes, marsupials, or multituberculates.

Almost the entire basisphenoid is preserved. The posterior continuations of the pterygoid ridges are seen, although the pterygoid bones themselves would appear to have been more anterior in position. The ridges diverge slightly as they pass posteriorly on the basisphenoid, neither increasing nor decreasing in prominence but

becoming flattened and ending on each side in a somewhat recurved, laterally projecting horizontal prominence lying just anterior to a large somewhat laterally placed foramen. This foramen probably lay between the basisphenoid and the alisphenoid or the periotic or both. Directly between these two foramina are two others, smaller, truly ventral rather than ventro-lateral, and piercing the basisphenoid itself. They are of unequal size, that on the right side being larger and circular and that on the left smaller and elongate. Beginning between these two smaller foramina and running forward is a median ridge, originally rather higher than the pterygoid ridges and dividing the space between the latter into two longitudinal grooves. The right side of this ridge is somewhat furrowed where the basisphenoid is widest. A small, nearly horizontal, plate of bone is seen attached to the right anterior end of the basisphenoid, external to the pterygoid ridge, and it probably represents a fragment of the fused alisphenoid, but no foramina occur in the part preserved.

Some doubt must unfortunately attach to the interpretation of so small a part

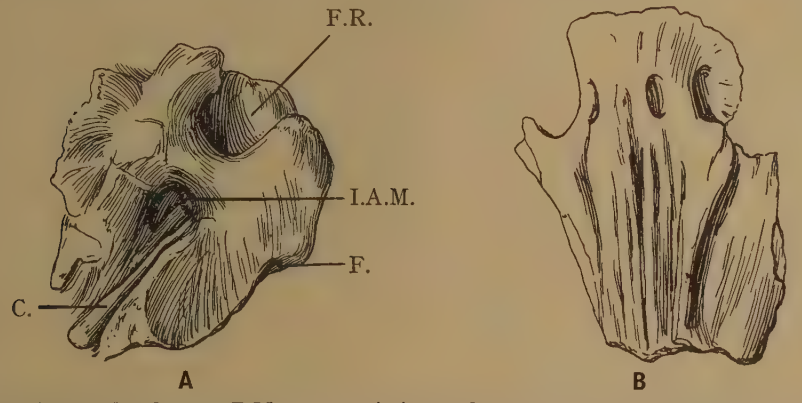


FIG. 25.—*Triconodon mordax* Owen. B.M. 47763. A, internal aspect of incomplete right periotic. B, lower aspect of basisphenoid, with a fragment of the right alisphenoid. C, cast of cochlear cavity. F, small foramen leading into inner ear. F.R., floccular recess. I.A.M., internal auditory meatus. Both considerably enlarged but not to scale.

of the skull of a mammal so much older than any other in which this element is known. Two of the most primitive recent animals, *Didelphis* and *Ornithorhynchus*, each present somewhat comparable features. Some specimens of *Didelphis* have basisphenoids apparently very much like that here described. If this agreement is truly structural, the small foramina wholly within the basisphenoid are for branches of the entocarotid and the two larger and more lateral openings pertain to the so-called transverse canal. If, however, we disregard certain obvious specializations, especially of the palate, the comparison with *Ornithorhynchus* seems to be a safer one. This would also make the smaller foramina the openings for the entocarotid, but would make the more lateral ones the foramina ovalia, as the latter occupy exactly this position in the Duck-bill. That this more median position of the foramen ovale and its close association with the entocarotid foramen may be primitive is also suggested by the relationships seen in many insectivores and some marsupials.

Both periotics are present, although neither is perfectly preserved. Both are

seen in internal aspect and since the left shows nothing not also seen on the more perfect right, the latter will be described. The edges of the bone are all broken and do not represent sutural contacts. The internal surface has a somewhat flattened surface in which two depressions are prominent: the floccular fossa and the internal auditory meatus. The latter is smaller and less deep. At its bottom is a rounded longitudinal ridge dividing it into an upper (anterior) and a lower (posterior) passage for the seventh and eighth cranial nerves respectively. Beginning below the latter, and continuing forward for a distance of approximately $3\frac{1}{4}$ mm., is the trochlear duct. This has a uniform diameter of about $\frac{1}{2}$ mm., and its anterior end is blunt and rounded. The cochlea was almost straight—a condition altogether unique among mammals and even more reptile-like than that seen in *Echidna*.

Posterior to the internal auditory meatus and at the edge of the specimen as preserved, is a small foramen which is probably that of the vestibular aqueduct, although from its position rather remote from the meatus and nearer the cochlea it might be the foramen for a cochlear aqueduct. If the latter, however, no vestibular aqueduct would be visible on the specimen.

The floccular recess and the internal auditory meatus are separated from each other by a large rounded bony ridge. The recess was unfortunately cut in half soon after the specimen was discovered, and the rest of this bone, as well as any other cranial elements which may have been present, was cut off and thrown away. The fossa apparently was circular and of considerable depth (now reduced by crushing) and the mouth was somewhat restricted. It thus resembles that of many primitive mammals, as *Ornithorhynchus, Didelphis, Potamogale;* and this type of deep and well-defined floccular fossa is probably an ancestral mammalian character. The anterior semi-circular canal which surrounds this recess, and hence should be seen in section on this specimen, cannot be made out. This is certainly due not to its absence, which would be impossible, but to its very minute size (it would be literally hair-like in so small an animal) and to its being filled with honey-coloured crystallized calcite not distinguishable from the bone itself. In bones occurring at this horizon this is usually true of small cavities not accessible to matrix.

Anterior and superior to the internal auditory meatus is the edge of a recess apparently comparable in size to that for the flocculus and with a rather sharp lip on the side toward the meatus. The part preserved contains no foramina.

Skeletal Remains.

On the same specimen as the skull bones, the axis is preserved. Only the inferior surface is visible. The odontoid is stout and peg-like, nearly circular in section but slightly depressed vertically. On each side are the articular facets which, if they were not interrupted by the odontoid, would form a complete semi-circle. The facets look more downward than forward. The lower surface of the centrum between them is concave and its posterior edge, as preserved, is a straight

transverse line between the posterior ends of the two articular surfaces; but this is probably a break and not the original posterior end of the centrum.

Associated with the atlas are several fragments of bone which present no peculiarities sufficient for their identification.

The only other bone on the slab is a slender limb bone which, from its sheer lack of character, one takes to be a radius. One end is present but so indifferently preserved as to be uncharacteristic. The length of the part preserved is 23 mm. and the minimum diameter 1·5 mm., indicating an animal with slender but well-developed fore-limbs.

Brain.

From the natural internal cast of the left parietal and the internal view of the left frontal, it is possible to make a reconstruction of the dorsal part of the endocranial cavity.

The olfactory lobes are relatively very large, triangular or subpyriform, dorsal in position, closely appressed to the cerebral hemispheres but not at all concealed or overlapped by the latter. Anterior to them the inner surface of the frontal indicates an expansion into a large nasal cavity and bears ridges corresponding to the bases of the turbinals. The specimen is not sufficiently complete to give much information as to the latter save that they clearly were well developed. Not less than four ridges are present on the strictly dorsal part of the frontal. Together with the large olfactory lobes, a strongly developed sense of smell is indicated, quite in keeping with the primitive character of the mammal and with the predatory nature of its dentition.

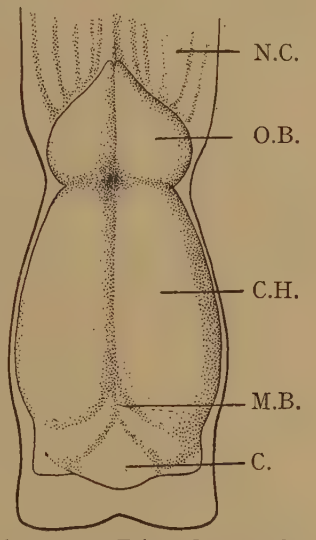


Fig. 26.—*Triconodon mordax* Owen. Reconstruction of dorsal aspect of endocranial cast from cranial fragments associated with B.M. 47763. C., vermis of cerebellum. C.H., cerebral hemisphere. M.B., midbrain. N.C., nasal chamber. O.B., olfactory bulb. × 3 diam.

The cerebral hemispheres as restored are long, narrow, and oval. The length and breadth may originally have been slightly different from that shown, but the difference cannot have been great. The superior surfaces of the hemispheres, at least, are quite free from convolutions. They are rather flat superiorly, not arched or expanded. Their posterior end is marked by a groove in the endocranial cast which is very shallow, as are all those marking off the topographical features of this brain. Parallel to this oblique groove and about 1 mm. from it is another even less prominent, marking the anterior and lateral limit of the vermis of the cerebellum. The vermis is about 3·5 mm. wide, and the part exposed beneath the parietal of about the same median length.

Between the vermis and the cerebrum antero-lateral to the former, and also posterior to the cerebrum and lateral to the vermis, is a region of very slight convex relief, probably corresponding to the lateral portions of the central cerebellar lobes. The pineal body has left no mark on the cranial roof.

The cast of the cerebellum ends abruptly posteriorly as the supraoccipital is

not preserved and, although this bone apparently did not form part of the skull top, yet even more of the cerebellum may have been visible from above when complete. In any event the dorsal exposure of the cerebellum is very large.

MEASUREMENTS.

Maximum lengths in millimetres.

Lower jaws—

	P_1.	P_2.	P_3.	P_4.	P series.	M_1.	M_2.	M_3.	M_4.	M_{1-3}.	M_{1-4}.
47764..	—	—	—	2·1	—	2·4	2·8	2·9	—	8·0	—
47763..	1·1	1·1	1·75	2·4	6·4	2·2	2·5	2·9	—	7·7	—
47771..	—	—	—	—	—	2·3	3·1	3·3	—	8·7	—
48395..	—	—	1·6	1·8	—	2·1	2·6	2·6	—	7·2	—
47767..	—	—	—	2·2	—	2·6	—	—	—	—	—
Willett	—	—	2·0	2·5	—	2·5	3·2	3·4	3·3	9·4	12·7

These measurements indicate a wider range in size than is sometimes admitted in a single species, especially in a fossil species, but if they are plotted, all these forms fall into a distinct group which cannot be definitely subdivided and which is evidently distinct from the other species of Purbeckian triconodonts. Bearing this fact in mind and also considering the morphological data, it does not seem necessary to erect any new species on this material.

Upper jaws—

	M^2.	M^3.	M^4.
47806	2·1	2·4	—
48396	—	2·4	1·75
47784	—	2·7	—

GENUS TRIORACODON nov.

(Text-fig. 19.)

DIAGNOSIS.—Triconodontinae with dental formula $I^3_3\ C^1_1\ P^4_4\ M^3_3$. Anterior and posterior cusps of lower molars a little lower relative to midcusp. M^3 reduced and bicuspid.

The name is derived from τρείς, three, ὄρος, mountain, ἀκή, point, ὀδούς, tooth, with analogy to its allies *Triconodon* and *Priacodon*.

GENOTYPE.—*T. ferox*.

DISCUSSION.—Owen (1871) believed that there were two genera of triconodonts in the Purbeck, one with three and one with four molars. He believed that his *Triconodon* (type *T. mordax*) had three molars and his *Triacanthodon* (*T. serrula*) four. Lydekker and Osborn believed that *Triacanthodon serrula* and *Triconodon mordax* were synonymous, a belief now fully confirmed, and therefore that *Triconodon* was characterized by four molars. Lydekker (1887, p. 258) suggested that M_4 was not always developed in *T. mordax*, also (p. 260) that this tooth was not known to occur in *T. ferox*. Osborn (1888A, p. 247) recognized this fact, and on that account suggested that *Triconodon* might really have only three molars ; but this was based on his erroneously taking *T. ferox* as the genotype. As a matter of fact, *Triconodon*

certainly has four molars in the adult state, as supposed by Lydekker and Osborn, and *Triacanthodon* is certainly synonymous with this genus. Since it now proves that *T. ferox* and its allies never had four molars and had other modifications distinguishing them generically from *T. mordax*, it follows that these species belong to a distinct genus, which has been defined above under the name *Trioracodon*.

Trioracodon ferox is selected as the genotype. The Purbeckian species *T. major* (Owen) and *T. oweni* (sp. nov.) are also referable to *Trioracodon*, as is also the Morrison species *Triconodon bisulcus* Marsh.

Trioracodon ferox Owen.

(Pl. V, figs. 6–7 ; Pl. VI, figs. 1–6 ; Text-figs. 27–30.)

1871. *Triconodon ferox* Owen, " Fos. Mam. Mesozoic," p. 64.

1871. *Triconodon occisor* Owen, " Fos. Mam. Mesozoic," p. 69.

See also Lydekker, 1887, p. 260 ; Osborn, 1888A, p. 195.

DIAGNOSIS.—P_2 relatively short and high. M_3 longer than M_2. Molar cusps relatively stout. Length of M_2 about 4·5 mm.

FORMATION AND LOCALITY.—Purbeckian of Durdlestone Bay, Swanage, Dorset.

MATERIAL.—All of the known specimens are in the British Museum, and all but one are from the Beckles Colln. (*Purchased* 1876.)

47775. Left ramus slightly broken, with bases of C and P_2 and crowns of P_{3-4} and M_{1-3}. Internal aspect. Holotype. Figd., Owen, 1871, pl. iii, fig. 11. It is the lower jaw, restored, in Osborn, 1888, pl. viii, fig. 4.

47765. Left ramus with M_{1-3} and part of the jaw anterior to them. External aspect. Figd., Owen, as *T. mordax*, 1871, pl. iii, fig. 8.

47772. Part of the right ramus with broken P_4 and M_1. External aspect. Figd., Owen, 1871, pl. iii, fig. 21.

47773. Left ramus, internal aspect, with one very badly preserved tooth. Figd., Owen, 1871, pl. iv, fig. 4.

47774. Part of left maxilla with a broken premolar and M^{2-3}. Figd., Owen, 1871, pl. iii, fig. 14.

47774*a*. Right ramus with C, P_4, and M_{1-3}, all badly crushed, but with the condyle and masseteric flange well preserved.

47776. Right ramus, external aspect, with M_{1-3} and much of the toothless jaw in front of this. Figd., Owen, 1871, pl. iii, fig. 12.

47777. Left ramus, external aspect, with badly broken P_4 and M_{1-2} and well-preserved M_3. Figd., Owen, 1871, pl. iii, fig. 13.

47778. Part of right maxilla with P^{3-4}, M^1 and part of M^2. Figd., Owen, 1871, pl. iii, fig. 17.

47779. Part of left maxilla with P^{3-4} and M^{1-2}. Figd., Owen, 1871, pl. iii, fig. 18.

47780. Fragment of right ramus, outer aspect, with M_3. Figd., Owen, 1871, pl. iii, fig. 19.

47781. Right ramus, inner aspect, with two incisors, C, P_{2-3} and M_2 visible. Associated left ramus, outer aspect, with C, P_{3-4} and M_2 visible. Right maxilla with M^2 visible. Left maxilla with a molar visible. Vertebrae and other bones, mostly unidentifiable. Figd., Owen, 1871, pl. iv, fig. 1.

47782. Left ramus, outer aspect with badly broken C, P_{1-4} and M_{1-3}. Associated right ramus, inner aspect, with broken C, P_{1-4}, M_1 and M_3. This is the type of *T. occisor*. Figd., Owen, 1871, pl. iv, fig. 2.

47788. Part of right maxilla, inner aspect, with C and P^{2-4}. Not figured as such but used as a basis for the anterior part of the upper jaw in Osborn, 1888, pl. viii, fig. 4.

47791. Part of right ramus, outer aspect, with broken M_{2-3} and with pterygoid and masseteric crests unusually well displayed.

48397. Left ramus without any teeth but apparently referable to this species.

48404*a*. Single premolar.

M 10474. Right maxilla with P^4 and M^{1-3}. Figd., Woodward, 1912, pl. xv. (*Presented by John Newton, Esq.*, 1910.)

Lower Dentition.

Tooth Growth and Formula.—Two incisors may be seen in 47781 and one or two more may have been present. The number of upper incisors is quite unknown. Canines are present, and four lower premolars are seen in the holotype and several other specimens. 47788 shows three upper premolars and space for another. M 10474 shows that there were not more than three molars in the upper jaw, as M^3 is reduced and its posterior portion lost. In view of the occlusal relationships in the group, this maxilla could not belong to an animal which ever had more than three lower molars, even in old age. There are six lower jaws in which the number of lower molars can be counted, and in each jaw it is three. To make this absolutely certain one of these jaws (47777) was exposed from the back and the bone behind M_3 dissected away cautiously, so that it is possible definitely to assert that not even an unerupted germ or formative capsule for an M_4 is present. The definitive dental formula, so far as yet known, is $I^1_1\ C^1_1\ P^4_4\ M^3_3$.

Deciduous teeth do not appear to be present in any of the jaws, but the course of the later stages of tooth-growth seem to have been much as in *Triconodon mordax*. 47782 is the youngest individual in the collection. In it the canines are not quite fully extruded, while P_4 is just beginning to appear. The anterior cusp of M_3 is exposed, but the middle cusp is half hidden and the posterior cusp is still entirely within the capsule. Even in older specimens the base of this third cusp is usually hidden. In the upper jaw 47788 P^4 is just beginning to emerge.

Incisors.—These are seen only on 47781, and even here only the most lateral

incisor is preserved. It is a small, insignificant tooth with a recurved tip, the postero-internal face excavated, and with a small posterior cingulum.

CANINE.—The canine is predatory in shape—large, high, sharp, recurved. The antero-external face is convex, the postero-internal separated from it by longitudinal angulations and flattened or even slightly concave near the edges. There appears to be only one root.

PREMOLARS.—The four premolars increase regularly in size but their characters are the same. There is a high laterally-compressed main cusp and a small posterior accessory cusp. There is no external cingulum, but a sharp continuous internal cingulum is present, rising slightly in the middle, where it is faintly crenulated, and

FIG. 27.—*Trioracodon ferox* (Owen). Composite reconstruction of external aspect of left upper and lower dentition. Only parts actually known are included. × 4 diam. Upper Jurassic, Middle Purbeck beds, Swanage, Dorset.

rising at the ends to form tiny anterior and posterior accessory cusps. The last premolar is somewhat higher than the succeeding molar.

MOLARS.—Both the premolars and the molars are very like those of *Triconodon mordax*. The cingula are more definitely nodulated and they rise to a small point on the anterior part of the base of the third cusp of each tooth, which they do not do in *T. mordax*. The anterior and posterior cusps are also a little lower relative to the mid-cusp—a difference which, though slight, appears to be constant. It is, however, less accentuated in this than in other species of *Trioracodon*.

The three molars increase slightly in size from anterior to posterior. Owen considered that in 47782, the type of his *T. occisor*, M_1 was smaller relative to M_{2-3} than in the other species, but this proves to be illusory, for, within the mechanical limits of error in comparison, the various tooth proportions of this specimen are those of *T. ferox*.

Lower Jaw.

The morphology of the lower jaw is closely similar to that of *Triconodon*. Owen characterized *T. occisor* and *T. mordax* by their more abrupt symphysial contour, but, as already suggested, this is of little importance.

47791 is a very important specimen, as it is the only triconodont known which shows the condyle, masseteric, and pterygoid crests complete. It fully confirms the inferences drawn from more fragmentary material (see especially Simpson, 1925 A, p. 155). The condyle itself is much elongated transversely, the pitted surface indicating that the joint itself was cartilaginous. As viewed from below, the jaw is widest at the condyle. From that level there run forward two nearly horizontal bony shelves, the broad masseteric crest externally and the much less developed pterygoid crest internally. They become narrower as they pass forward, and they end at the anterior extremities of the masseteric and pterygoid fossas respectively, just behind the last molar. There is no angular process or any structure homologous there with an angular process.

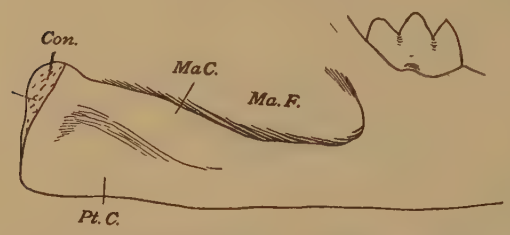


Fig. 28.—*Trioracodon ferox* (Owen). Somewhat oblique external view of the postero-inferior part of the right mandibular ramus. Based on B.M. 47791. *Con.*, articular condyle. *MaC.*, masseteric crest; *Ma.F.*, masseteric fossa. *Pt.C.*, pterygoid crest. × 3 diam.

47765, 47772 and 47782 have each two mental foramina, one beneath P_2 and one beneath P_1, varying a little in exact position. In 47776 these two foramina are visible, and there may be another anterior to them, although the crushed condition of the specimen renders this uncertain.

The symphysial surface extends back to a point beneath the posterior end of P_2. The internal groove is very poorly developed. In the holotype, 47775, there is a definite groove beginning beneath the posterior root of M_3, about 4·5 mm. in front of and below the dental foramen, and running forward for a distance of only 5 mm. to a point below M_2, keeping parallel to the lower border and a little over 1 mm. from it. Near the symphysis there is a faint suggestion of a groove, but it is very indefinite and would not be continuous with the other if produced posteriorly. In 47773 there is a very faint groove, only to be seen with strongly oblique light. It begins in about the same position as that of the holotype and then curves forward, at first receding from the lower border and then parallel to it, being barely distinguishable for about 10 mm.

In 47775 the pterygoid fossa is well shown. It is very shallow, its anterior end grading indefinitely into the general inner surface of the horizontal ramus. The dental foramen, in this specimen at least, is not of the usual smoothly rounded type, but is an elongated slit-like opening, with ragged edges, in the bottom of the pterygoid fossa near its anterior end. The pterygoid crest is slight.

Upper Dentition.

Canine.—The superior canine is seen in lateral aspect in [illegible]. The form may possibly be the deciduous canine as P¹ is just cutting the gum in the individual. It tapers rapidly to a sharp recurved point. The postero-internal face is somewhat flattened and is bounded longitudinally next to the angulations which separate it posteriorly and antero-externally from the antero-external face of the tooth. The base is much enlarged antero-posteriorly and transverse to form two stout divergent roots.

Premolars.—P¹ is nowhere present in single or more or worn. P²⁻⁴ are essentially alike save for progressive increase in size and must resemble the lower premolars. There is the same laterally compressed crown-cusp with small posterior accessory cusp and still smaller anterior and posterior cingulum cusps. The internal cingulum is sharp and continuous, rising slightly on the main cusp. Unlike the lower premolars, there is also an external cingulum. On P² seen in [illegible] it is confined to the region below the posterior accessory cusp. On P³ it extends forward to the middle of the tooth but a descent anterior value on P⁴ [illegible] it is continuous along the outer surface of the tooth. In all cases it is rather irregular and crenulated.

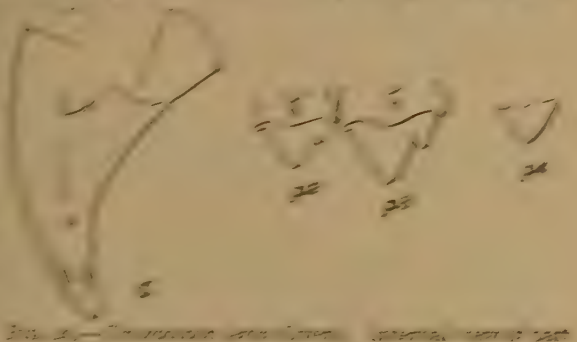


Fig. 2.—Triconodon sp. (cf. [illegible]), type of right upper dentition, B.M. [illegible]. ×6 diam.

Molars.—The first two molars are very similar save that the second is larger. There is a continuous but irregular and strongly crenulated outer cingulum. It rises very feebly anteriorly to form an antero-external cuspule and very slightly posteriorly up to the middle and highest portion of the longitudinal series. The outer face of the first cusp distal to the cingulum is concave that of the second and third cusps gently convex. The outer surfaces of the last two cusps are not well differentiated from each other on M² but on M³ they are separated by a narrow vertical groove followed on the anterior part of the third cusp by a slight vertical ridge. The cusps of each tooth are separated at their apices by rounded notches, the posterior somewhat deeper as is familiar in other triconodonts. In lateral aspect the cusps is conical and columnar and separated by more or less vertical valleys. There was an internal cingulum but the specimens available are too worn to determine to exact development.

As pointed out in Smith Woodward (1901) P⁴ is quite differently developed. It is reduced in length, with only two volumes instead of the three of the normal molar, and even the second of these is reduced in relative size. The outer face of the first cusp is concave and there is a slight cingulum below it, but not below the gently convex outer face of the second cusp. There is a distinct internal cingulum below the first, but not the second, cusp. The tooth is triangular in outline being

narrower posteriorly. As already pointed out elsewhere (Simpson, 1925 A, p. 354), this reduction of the third upper molar is related to the fact that there were but three lower molars. The last cusp of M_3 occluded between the first and second columns of M^3. The third column of M^3 was thus functionless, became reduced and finally lost.

The specimen (M 10474) which enabled Smith Woodward to reveal this unexpected character of M^3 was found in 1910. There had, however, long been another specimen in the collection which showed the same thing, although a little less clearly. This is 47774, which unfortunately has hitherto been interpreted as a lower jaw. M^2 of this specimen is a little larger than in M 10474 but otherwise similar. M^3 is unworn and therefore has quite a different aspect, but the structure is the same. The notch in the crest between the first and second cusps is due to wear from the lower molars and does not occur in this unworn tooth. The crest

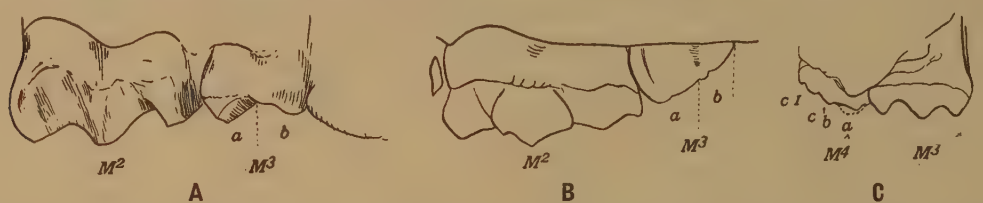


FIG. 30.—*Trioracodon ferox* (Owen) and *Triconodon mordax* Owen. A, *T. ferox*, B.M. Reg. M 10474, internal view of last two upper molars. B, *T. ferox*, B.M. Cat. No. 47774, external view of last two upper molars. C, *T. mordax*, B.M. Reg. 48396, external view of last two upper molars. *a*, *b*, *c*, c^1, columns of last molar. All × 6 diam. Upper Jurassic, middle Purbeck beds, Swanage, Dorset.

is also much higher and thinner, and the whole tooth seems to be a little narrower, although it may have been equally wide when fully protruded and worn.

SKULL.

The small process of the maxilla posterior and external to the last molar, and the longer, tapering zygomatic process are well seen in M 10474, and are much as in *Triconodon mordax*. The anterior border of the orbit was slightly anterior to M^1. The infra-orbital foramen is larger, apparently single, and is a short distance above P^2. The lateral emargination of the palate extends forward near to the anterior end of M^2; in 47779 part of the anterior and lateral edge of a large palatal vacuity may be seen opposite P^4 and the anterior end of M^1.

MEASUREMENTS.

Maximum lengths in millimetres.

LOWER JAWS:

	P_2.	P_3.	P_4.	M_1.	M_2.	M_3.	M_{1-3}
47775	—	2·4	3·2	3·4	4·6	5·1	13·1
47765	—	—	—	3·6	4·3	—	—
47776	—	—	—	3·7	4·7	—	—
47777	—	—	—	—	4·8	5·0	—
47782	1·7	3·5	—	3·4	4·4	—	—

UPPER JAWS:

	P_2.	P_3.	P_4.	M_1.	M_2.	M_3.
47774 ..	—	—	—	—	4·9	3·0
47778 ..	—	3·1	3·6	4·3	5·0	—
47779 ..	—	2·8	3·3	4·0	—	—
47788 ..	2·0	2·7	—	—	—	—
M 10474 ..	—	—	3·7	4·0	4·3	2·9

Trioracodon oweni sp. nov.

(Pl. VI, fig. 7; Text-fig. 31.)

DIAGNOSIS.—P_2 relatively long and low. M_3 markedly shorter than M_2. Molar cusps somewhat more slender. Length of M_2 about 3·2 mm.

FORMATION AND LOCALITY.—Purbeckian of Durdlestone Bay, Swanage, Dorset.

MATERIAL:

47766. Right mandibular ramus, internal aspect, with entire crowns of P_2 and M_{2-3}, broken crown of M_1, and roots of P_1 and P_{3-4}. Holotype. Figd., as *Triconodon mordax*, Owen, 1871, pl. iii, fig. 9. (*Beckles Colln. Purchased* 1876.)

LOWER DENTITION.

PREMOLARS.—Only P_2 is preserved, but it is characteristic. It is notably longer and relatively lower than in *T. ferox*, with the internal cingulum absent

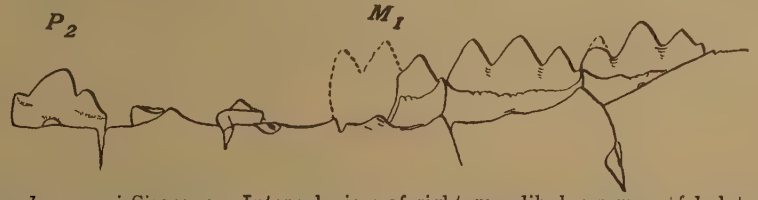


FIG. 31.—*Trioracodon oweni* Simpson. Internal view of right mandibular ramus of holotype. × 6 diam. Upper Jurassic, middle Purbeck beds, Swanage, Dorset.

anteriorly and faint and rounded posteriorly. The anterior cingulum cusp is distinct and almost as high as the posterior accessory cusp, but the posterior cingulum cusp is obsolete. The central cusp is small and recurved.

MOLARS.—It is certain that there were only three molars, as the jaw is broken behind M_3 in such a way that M_4 would be revealed if present. M_3 is smaller than M_2 as it is in *T. bisulcus* and in noteworthy contrast to *T. ferox*. The shape of the molar cusps also approaches that of the American species. They are more slender than in *T. ferox*, with anterior and posterior contours straight rather than convex. The anterior and posterior cusps are slightly but distinctly smaller than the central cusp. The internal cingulum is crenulated and is continuous, although it is a little weaker on the midcusp. It rises slightly between the anterior cusp and the central one, and again between the latter and the posterior one. There is a small posterior cingulum cusp.

Although the species is quite distinct, it is interesting to note that its molars approach those of the American *Trioracodon bisulcus* in several respects and tend to link that form with the genotype, *T. ferox*.

MEASUREMENTS.

Maximum lengths in millimetres :

	P_2.	P_3.	P_4.	M_1.	M_2.	M_3.
47766	2·1	—	—	—	3·2	2·8

Trioracodon major Owen.

(Pl. VII, fig. 1.)

1871. *Triconodon major* Owen, " Fos. Mam. Mesozoic," p. 70.

DIAGNOSIS.—M_2 about 5·5 mm. in length. The whole jaw about one-third larger than in *T. ferox*.

FORMATION AND LOCALITY.—Purbeckian of Durdlestone Bay, Swanage, Dorsetshire.

MATERIAL.—The following specimen is in the British Museum :

40722. Right ramus, outer aspect, with fragmentary P_4 and M_2. Holotype and only specimen. Figd., Owen, 1871, pl. iv, fig. 3. (*Purchased.*)

This species is based purely on the difference in size, as the type is too imperfect to yield other criteria. That the species is probably valid is indicated by the fact that the various specimens of *T. ferox* form a fairly compact group as regards size and that there are no known intermediates between that group and *T. major*. Better material is needed, however, before the species can be placed on a truly sound basis. It is of considerable interest as being the largest known Jurassic mammal.

DENTITION.

P_4 is represented by its base, but no morphological data can be derived from it. M_2 is present but the apices of the first and second cusps are broken off. The outer base of the crown below these cusps is little differentiated. An unusual feature is the presence of an irregular row of crenulations along the basal swelling—the nearest approach to an external cingulum yet observed in the triconodont lower molar. There is a small posterior cingulum cusp.

There are alveoli for M_3 and it seems quite certain that the total number of molars was three.

MANDIBLE.

The mandible is of the familiar triconodont type, but is very striking on account of its relatively great size. The great efflected masseteric flange so characteristic of the triconodontines is well shown. The saw-cut which brought about the discovery of the specimen passed through it just behind M_3.

MEASUREMENTS.

40722 : Length of M_2 .. .. 5·5 mm.
Depth of ramus below M_2 outside .. 10·5 mm

Triconodontinae inc. sed.

The following two specimens from the Purbeckian of Durdlestone Bay are triconodontine but unidentifiable as to genus or species.

Both are in the British Museum and from the Beckles Colln., purchased 1876.

47797. Part of a left maxilla with broken posterior tooth fragments and an associated natural mould of part of the internal surface of the right frontal.

47807. Single anterior premolar.

The first specimen listed is important as showing part of the brain cavity. Except for its slightly larger size it agrees with that described above and furnishes no additional information. The fragments of teeth present are clearly triconodont, but not further identifiable.

The isolated premolar listed under 47807 is unidentifiable and of no importance.

Order SYMMETRODONTA Simpson.

Diagnosis.—Mammalia with the lower molars nearly or quite symmetrical with respect to a transverse median plane, a high centro-external cusp and lesser anterior and posterior inner cusps, a well-developed internal cingulum below these internal cusps, sometimes a slight external cingulum. There is never a true heel or talonid. Upper molars with a high centro-internal cusp and anterior and posterior external cusps on its slopes, with an external but no internal cingulum. Mandible with slight pterygoid crest but no angular process. Condyle rounded, not strongly transverse, and above the alveolar level.

Discussion.—The unique features of the few known members of this group are only now beginning to be appreciated. They were long obscured by the belief that the creatures were slightly modified triconodonts, whereas in fact they are fundamentally distinct from that group and no intermediate stages are known. Owen (1871) did not erect any families, but he placed *Spalacotherium* with the pantotheres in a group of multidentate marsupials with more than two mandibular incisors. Marsh (1887, p. 340) formed the family Spalacotheriidae for *Spalacotherium* and *Menacodon*—the latter genus being a synonym of *Tinodon*, which, strangely enough, he placed in a separate family, the Tinodontidae. Here he also placed *Phascolotherium*, a triconodont, thus beginning the confusion between the two groups which has lasted ever since. Osborn's classification (1888) has the same grouping of genera, differing only in making Marsh's two families subfamilies of the Triconodontidae (under the names Phascolotheriinae and Spalacotheriinae). The last classification of this high authority (1907) differs only in placing the Spalacotheriinae as Triconodonta Incertae Sedis. In 1910 (p. 174) Gregory retained the symmetrodonts with the Triconodonta, as he also did in 1922, with a query, whereas in the same work (p. xiii)

Matthew recognized their fundamental distinction from the triconodonts and suggested that they might be pantotheres, but neither of these authors revised the classification of the group itself. Recently the American forms have been restudied and revised (Simpson, 1925B), the identity of *Menacodon* with *Tinodon* pointed out, a new genus *Amphidon* described, and referred to the new family Amphidontidae, and *Tinodon* and *Spalacotherium* placed in the family Spalacotheriidae Marsh. The present study strongly confirms this taxonomic disposition of the group and it is here retained, the only innovation being that *Peralestes*, which was then left incertae sedis or a very doubtful amphidontid, is now definitely referred to the Spalacotheriidae. The Amphidontidae are unrepresented in Europe as yet, and do not enter into the present memoir.

Family SPALACOTHERIIDAE Marsh.

Diagnosis.—Symmetrodonta with lower molars functionally tricuspid. Antero- and postero-internal cusps distinct and well developed, springing from base of crown. Internal cingulum continuous, rising to form small anterior and posterior cingulum cusps.

Discussion.—To this family are referred the genera *Spalacotherium*, *Tinodon*, and *Peralestes*. All are from the uppermost Jurassic, *Tinodon* from Wyoming, and the other two from Durdlestone Bay, Dorset. *Peralestes* is based on an upper jaw, and is probably synonymous with *Spalacotherium*, although there is sufficient doubt about this for the name to be retained for the present. *Spalacotherium* and *Tinodon* are related but quite distinct, as will appear below.

Genus SPALACOTHERIUM Owen, 1854.

1854. *Spalacotherium* Owen, *Quart. J. Geol. Soc.*, London, X, p. 426.

Diagnosis.—Spalacotheriidae with dental formula $I_{?3} . C_1 . P_3 . M_7$. Molars higher than long, external cingulum present. Premolars definitely recurved and asymmetrical. Coronoid arising at an angle of about 60° to the alveolar border.

Discussion.—The only genus which can be closely compared with this is *Tinodon* Marsh. The two may be contrasted as follows:

Spalacotherium. $I_{?3} . C_1 . P_3 . M_7$.	*Tinodon.* $I_? . C_1 . P_3 . M_4$.
Canine moderate, erect.	Canine small, procumbent.
Premolars recurved, asymmetrical.	Premolars symmetrical, three-cusped, not recurved.
Length of molars along cingulum less than height above it.	Molars longer than high.
Weak external cingulum.	No external cingulum.
Coronoid rising at about 60° to alveolar border, relatively slender, recurved.	Coronoid rising at 90° to alveolar border, very broad, not recurved.

Too little is known of the group to give a valid basis for estimating the more or less primitive nature of these various characters. In general one may say that

they stand at about the same evolutionary level. The molars are very closely comparable except in proportions, and these seem to depend on the reduction of the molar number in *Tinodon*—this genus therefore is probably more specialized as regards the molars. On the other hand, general considerations might lead us to believe that it is the more primitive in the character of its premolars. The reduction of the canine in *Tinodon* is probably a specialization, as a large canine is certainly primitive for the mammals generally. The characters of the mandible cannot be evaluated even in this uncertain fashion.

Owen included the two species *S. tricuspidens* and *S. minus* in *Spalacotherium*. Osborn (1888B) stated that *S. minus* was really a pantothere of the genus *Peramus*, a conclusion which the present study fully confirms. The genotype is therefore the only valid known species of the genus.

Spalacotherium tricuspidens Owen.

(Pl. VII, figs. 2–6; Text-figs. 19–32.)

1854. *Spalacotherium tricuspidens* Owen, *Quart. J. Geol. Soc.*, London, p. 426.
See also Owen, 1871, p. 21; Lydekker, 1887, p. 292; Osborn, 1888A, p. 203.

DIAGNOSIS.—The only known species of the genus. Median molars about 1·6 mm. long.

FORMATION AND LOCALITY.—Purbeckian, Durdlestone Bay, Swanage, Dorset.

MATERIAL.—All the known specimens are in the British Museum, and all, except 46019, from the Beckles Collection. (*Purchased* 1876.)

46019. Part of the left ramus, outer aspect, with M_{4-7} and impressions of other teeth anterior to them. This specimen was the first Purbeckian mammal found. Holotype. Figd., Owen, 1854, fig. 1; 1871, pl. i, fig. 32. (*Purchased* 1874.)

47748. Left ramus, outer aspect, alveoli for three incisors, for *C* and for P_1. Crown of P_2 and fragment of P_3. Impressions of the molars. Figd., Owen, 1871, pl. i, fig. 35.

47749*a*. Right ramus, outer aspect. M_{2-3} and roots of M_{4-7}. Impressions of *C*, P_{1-3} and M_1. Figd., Owen, 1871, pl. i, fig. 37.

47749*b*. Right ramus, inner aspect, with P_{2-3} and M_1. Figd., Owen, 1871, pl. i, fig. 36.

47750. Left ramus, internal aspect with M_{3-7} and post-molar region almost complete. Figd., Owen, 1871, pl. i, fig. 38; Osborn, 1888A, pl. viii, fig. 7.

M 5633. Left ramus, inner aspect, with *C*, P_{1-2} and impressions of other teeth. When figured by Owen the third premolar and first two molars were also preserved, but the piece containing them has since been broken away and lost. Figd., Owen, 1854, fig. 11, and 1871, pl. i, fig. 34.

Univ. of Arizona Library

Owen figured one other specimen (1871, pl. i, fig. 33) which was by far the best of all available to him, but repeated search has failed to find this specimen in the British Museum, and it is sadly evident that it is lost, probably having disappeared in the five years between the publication of Owen's monograph and the acquisition of the Beckles Collection by the Museum.

Dentition.

Dental Formula.—Owen believed all the cheek teeth to fall into one morphological series, and he speaks of ten molars. Osborn (1888A) pointed out that the premolars were quite distinct and gave the formula as $I_{3+} . C_1 . P_4 . M_{6?}$ Unfortunately there is now no single specimen in which all the molars or all the premolars are preserved. 47749*b*, however, shows what is clearly M_1 preceded by two premolars, while in M 5633 there is a canine followed by two premolars, of which the second is clearly the homologue of the first preserved in 47749*b*, indicating P_3 as definitive. In 47749*a* impressions of the anterior cheek teeth clearly show three premolars and no more. M 5633 contained all the premolars when figured by Owen, although the posterior premolar and the anterior molars are now missing. It is sometimes necessary to emend the more minute details of Owen's descriptions, but in its broader features his work in his monograph is uniformly trustworthy, and there can be no doubt from this figure (1871, pl. i, fig. 34B) that the fourth postcanine tooth was molariform. The subject of Owen's pl. i, fig. 33, also clearly had three premolars and seven molars, although this specimen is lost. The dental formula may thus be written with confidence as $I_{3+} . C_1 . P_3 . M_7$.

Incisors.—The incisor crowns are not preserved, but in 47748 there are three incisive alveoli in a longitudinal series anterior to the canine alveoli, and there may have been another incisor somewhat more median in position.

Canine.—The canine, now seen only in M 5633, is a tooth of moderate size implanted by two stout roots. The crown is somewhat compressed transversely, and the internal surface is somewhat concave vertically. The tooth is erect, with slightly recurved apex. There is an anterior angulation or cutting edge.

Premolars.—The three premolars conform in general type to those already seen in triconodonts and to be seen again among pantotheres. This form clearly was a fundamental one—indeed it is closely approached in a number of cynodonts and no doubt even preceded the mammalian organization. It is, however, somewhat different from that seen in *Tinodon* or in the Stonesfield triconodonts.

The premolars have a high, somewhat recurved, shearing main cusp, especially sharp and slender in P_{2-3}, with a small posterior accessory cusp and tiny anterior and posterior cingulum cusps. There is an internal cingulum, rising somewhat in the middle. There is also an external cingulum—a most unusual character in lower premolars of this type. The three premolars are progressively taller, the last slightly overtopping the succeeding first molar.

Molars.—Except for M_7, which is shorter, the molars are all of about the same length, but they increase in height both ways to M_4. The crown consists of three cusps: a large centro-external and two subequal lower internal. The arrangement

is nearly but not quite symmetrical. The crest from the main cusp to the postero-internal cusp is a little more nearly transverse, a little less oblique, than that which runs from the main cusp to the antero-internal one. The tooth as a whole is slightly but distinctly inclined forward, and there is a suggestion of being recurved about the main cusp, its posterior contour being nearly straight and its anterior one slightly convex. These suggestions of asymmetry are very slight in themselves and have not received previous attention. They are very faint or quite absent in the American forms. They must be emphasized, however, for, as will appear below, they have a vital bearing on the relationships of *Peralestes* and on the affinities of the group as a whole.

All the cusps are fairly slender and piercing. The main cusp is convex externally, and sends two sharp shearing edges inward, one to each internal cusp. The internal face of this cusp is flattened between these crests, and indeed slightly concave next to them, making them very sharp. The inner cusps spring upward and somewhat inward from a common base with the main cusp.

These molars are unique among Jurassic mammals in that each has a continuous cingulum passing completely round the tooth. Internally the cingulum maintains about an even level, swinging gently upward in the middle and rising slightly at the ends to form minute antero- and postero-internal cingulum cuspules, the posterior one apparently usually a little larger. From these cuspules the cingulum passes externally, becoming lower as it does so, and reaches its lowest point postero-externally. The cingulum is not very wide, but is sharp and un-nodulated throughout.

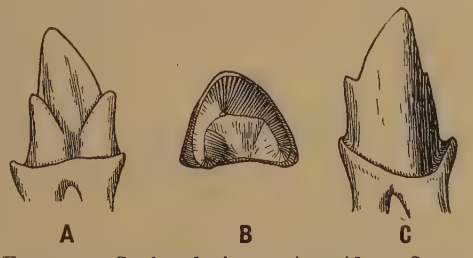


FIG. 32.—*Spalacotherium tricuspidens* Owen. Left lower molar. A, internal view. B, crown view. C, external view. × 10 diam. Upper Jurassic, middle Purbeck beds, Swanage, Dorsetshire.

The mouths of the alveoli are lower externally, as is usually the case, making the tooth appear higher in this aspect. There are two roots, both visible from inside or outside, but the anterior rather smaller and not extending quite so far externally.

The last molar is both shorter and lower than those preceding, its cingulum is obsolete externally, and the postero-internal cusp apparently is reduced relative to the others.

MANDIBLE.

The horizontal ramus is long and slender, the alveolar border perfectly straight, the lower border formed by a simple convex curve reaching its lowest point beneath the last molar. This curve, which is more pronounced posteriorly than anteriorly, is continued backward to the condyle by the line of the pterygoid crest. This latter, as seen quite well on 47750, is sharp but rather low, and the mandible resembles that of the multituberculates, and the triconodonts in being devoid of an angular process. Above the pterygoid crest is the shallow and ill-defined pterygoid fossa, with the dental foramen at its anterior extremity. From a point just below the dental foramen a well-marked internal groove starts, curving downward and forward

to become obsolete beneath the middle molars. The masseteric fossa is deep and has very definite antero-superior and anterior limits. Below it is the wide, efflected, flange-like masseteric crest. The coronoid process does not curve upward from the last molar, as in most mammals, but rises abruptly from the alveolar border at an angle of 60° or 70° to it, and about 2·5 mm. behind M_7. This at once recalls the similar condition in *Tinodon*, where the angle is even more abrupt. The coronoid is not as stout as in the latter genus and is recurved, with a distinct and relatively large supracondylar notch. The actual articular surface of the condyle is not preserved, even in 47750, but it was apparently much as in *Tinodon*, looking as much upward as backward, and raised well above the alveolar level.

The symphysial surface is not well shown, but appears to have extended back to beneath P_1. In 47748 two small mental foramina are seen, one beneath the anterior root of the canine and one beneath P_1.

MEASUREMENTS.

Maximum lengths in millimetres :

	C.	P_1.	P_2.	P_3.	M_1.	M_2.	M_3.	M_4.	M_5.	M_6.	M_7.
46019	—	—	—	—	—	—	—	1·6	1·6	1·6	1·1
47748	—	—	1·6	—	—	—	—	—	—	—	—
47749A	—	—	—	—	—	1·7	1·6	—	—	—	—
47749B	—	—	1·6	1·5	1·6	—	—	—	—	—	—
47750	—	—	—	—	—	—	1·7	1·6	1·6	1·6	1·0
M5633	1·4	1·4	1·6	—	—	—	—	—	—	—	—

The specimens show no measurable differences in size, and the species would appear to have been little variable.

GENUS PERALESTES Owen, 1871.

1871. *Peralestes* Owen, " Fos. Mam. Mesozoic," p. 33.

PROVISIONAL DIAGNOSIS.—A genus based on upper teeth possibly belonging to *Spalacotherium*. The molars are six in number and each has a high internal cusp with small antero- and postero-external accessory cusps, and an external cingulum outside these, the crown being asymmetrically triangular and about as wide as long.

GENOTYPE.—*P. longirostris* Owen.

DISCUSSION.—This genus has had a rather checkered career and it is with some relief that we find it now possible to give it a systematic position which seems likely to prove definitive. While basing the genus on the upper jaw (1871, p. 33), Owen also referred to it (with the alternative name of *Phascolestes*) a lower jaw of the dryolestid type, showing that he believed its affinities to lie with the forms which we now call pantotheres. Lydekker (1887, p. 294) suggested that the upper jaw in question probably belonged to *Spalacotherium*, basing this conclusion on the entirely erroneous grounds of fancied resemblance to *Chrysochloris* in upper and lower jaws. Osborn (1888A, p. 207) reverted to Owen's view, although he held that *Peraspalax* and not *Phascolestes* represented the lower dentition to be correlated. In his paper

of correction in the same year (1888B, p. 298), however, Osborn accepted Lydekker's view, although on strictly morphological grounds, as he recognized the fallacious nature of the analogy drawn by Lydekker, and this conclusion he retained in his final classification of the group (1907, p. 22). Gregory (1910, pp. 174–6) devoted a lengthy and ingenious argument to proving that *Peralestes* must be a pantothere, and in the lack of a re-examination of the originals this work seemed conclusive. At the time of his examination of the specimens in 1920, however, W. D. Matthew was convinced that the view of Lydekker, which was also the second view of Osborn, was correct and that *Spalacotherium* and *Peralestes* are the same type.

Re-examination of the morphology of the various types concerned seems to place this conclusion beyond reasonable doubt. The greatest difficulty in correlating *Peralestes* and *Spalacotherium* has always been that the former is obviously asymmetrical, while the latter was supposed to be symmetrical in its molar structure. If this were really the case they could not possibly belong together. If we examine a lower molar of *Spalacotherium*, as has been done above, we find :

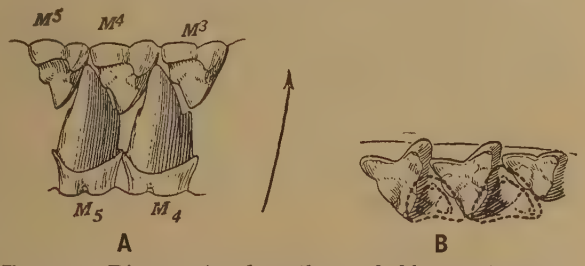


FIG. 33.—Diagram to show the probable association of the lower teeth known as *Spalacotherium* and the uppers known as *Peralestes*. A, external view of molars coming into occlusion. B, crown view of *Peralestes* molars, with diagram of *Spalacotherium* molars superposed to show occlusion. Both × 6 diam.

1. It is a shearing tooth with a high external apex. It would require an upper molar which was also a shearing tooth with a high internal apex. *Peralestes* has such teeth.

2. It is not symmetrical, but points slightly forward and the posterior shearing edge is the more directly transverse one. It would require upper molars which pointed slightly backward and had the anterior shearing edge the more directly transverse one. This also is true of *Peralestes*.

3. It has sharp antero- and postero-internal accessory cusps, but no centro-internal one. It would require upper molars with antero- and postero-external accessory cusps to continue the shearing edges and increase their mechanical efficiency, but one would not expect the upper molars to have a centro-external cusp. *Peralestes* again fills the requirements.

Peralestes is thus such a type as one would necessarily imagine for the upper dentition of *Spalacotherium*. If drawings of the crown views of the two dentitions are superposed, the *Spalacotherium* molars are found to fit quite well into the *Peralestes* interdental embrasures and *vice versa* (Fig. 33).

The next piece of evidence is less direct but of much value nevertheless. A number of different types of pantothere upper dentitions are now known, especially from the Morrison, but also from the Purbeck. These unquestionably belong to the Pantotheria and just as clearly are quite remote from *Peralestes*, which therefore seems unlikely to be a pantothere.

All these items of evidence lead me to place *Peralestes* in the family *Spalacotheriidae*. It is not to be definitely considered as a synonym of *Spalacotherium*,

however, until their association can be considered proven beyond any question. The only known specimen which compares at all closely with *Peralestes* is the single molar from the Morrison formation, which has been referred to *Amphidon* under the name *A. aequicrurius* (Simpson, 1925B, p. 463). The basic type is clearly the same in this form and in *Peralestes*, and it may eventually prove that the reference of the Morrison specimen to the Amphidontidae is incorrect and that it, too, should be among the spalacotherids. The forms differ as follows :

	Peralestes.	*Amphidon aequicrurius.*
1.	Crown about as wide as long.	Crown much longer than wide.
2.	Markedly asymmetrical.	Nearly symmetrical.
3.	Outer contour distinctly notched in the centre.	Outer contour nearly straight.
4.	Only one distinct cusp postero-external to the main one.	Two distinct cusps postero-external to the main one.

The first and third differences are not in themselves of more than generic value. The last is less important than appears at first sight, for the more postero-external of the two cusps in *A. aequicrurius* is very small and there is a very faint indication of a cusp here on M^{3-4} of *Peralestes*. The second difference is not, perhaps, vital in itself, but one would tend to attach much weight to it as demanding a quite different type of lower molar. This loses all significance, however, when we remember that, while *Spalacotherium* and *Tinodon* certainly are related and have lower molars of the same type, those of the former are much less symmetrical than those of the latter. One therefore concludes that *Peralestes longirostris* and *Amphidon aequicrurius* belong to two separate but related genera and that both represent the upper dentition of symmetrodonts.

Peralestes longirostris, Owen.

(Pl. VII, fig. 7 ; Text-fig. 33.)

1871. *Peralestes longirostris* Owen, "Fos. Mamm. Mesozoic," p. 33.
See also Osborn, 1888A, p. 205, 1888B, p. 298 ; Lydekker, 1887, p. 294 ; Gregory, 1910, p. 174.

DIAGNOSIS.—The only known species of the genus. Length of molar series about 8·7 mm.

FORMATION AND LOCALITY.—Purbeckian of Durdlestone Bay, Swanage, Dorset.

MATERIAL.—The following specimen is in the British Museum :

47740. Part of right upper jaw with the last premolar and all the molars and part of the jaw anterior to these teeth. Holotype and only specimen. Figd., Owen, 1871, pl. ii, fig. 3 ; Osborn, 1888A, pl. viii, fig. 8, 1907, fig. 12 ; and (with hypothetical and erroneous lower teeth) Gregory, 1910, fig. 9. (*Beckles Colln. Purchased* 1876.)

DENTITION.

DENTAL FORMULA.—Any conclusions based on the anterior alveoli are to some extent invalidated by the long space where all the bony alveolar process is broken

away. I cannot agree with Osborn's interpretation of this region (1888A, pl. viii, fig. 8). The alveoli which he marks "i" and "c" are now broken away, but both were almost surely incisive alveoli. The anterior alveolus which he considers to be for P^1 is merely a shallow pit into which the lower canine fitted—a precanine diastema. The posterior alveolus of his P^1 is properly part of the succeeding alveolus, the specimen here being spread somewhat by crushing. The two alveoli which he believed to belong to P^2 are quite clearly those of a large two-fanged canine, and the roots are notably larger than would appear in the earlier figure. The anterior alveolus for P^1 is preserved; behind this the specimen is broken, but it is obvious that there is space here only for the posterior root of P^1 and the two roots of P^2. The last premolar, which is preserved, is thus quite surely P^3. There was no long diastema in front of this tooth, as shown by Osborn, this space being occupied by P^2. The dental formula is thus $I^{2+} . C^1 . P^3 . M^6$, differing from that of the *Spalacotherium* lower jaw only in having one less molar, as might readily be the case in the upper jaw of the same type. The last lower molar is reduced, and especially its posterior part, and this is even more strikingly true of *Tinodon*.

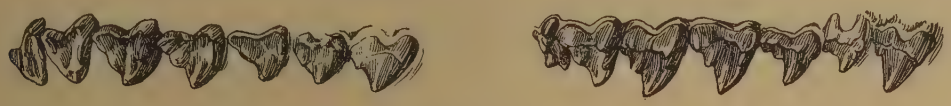


FIG. 34.—*Peralestes longirostris* Owen. Last premolar and all molars of holotype. A, slightly oblique crown view. B, external view. Both × 6 diam. Upper Jurassic, middle Purbeck beds, Swanage, Dorset.

Apparently the last lower molar in this group occluded behind the last upper molar.

PREMOLARS.—Only the last premolar, which we take to be P^3, is preserved. This tooth is a little higher than the loftiest molar (M^4) and consists essentially of a single high cusp, somewhat compressed laterally. There is a sharp continuous external cingulum running obliquely across the base of the outer face, being nearer the alveoli posteriorly than anteriorly. It is slightly crenulated but does not form any true cusps. Above the cingulum posteriorly is a small posterior accessory cusp.

MOLARS.—The six molars are all present. The first five are identical save in proportions and size. M^1 to M^5 are progressively wider and relatively shorter, M^1 being distinctly longer than wide, M^5 wider than long, but the cusp pattern is the same.

The crowns are triangular with the outer border placed, not parallel, but oblique to the alveolar border of the maxilla, the postero-external angle being more internal than the antero-external one. The anterior border of the crown is almost at right angles to the alveolar margin, and hence at an acute angle to the outer border. On M^{1-3} this side of the crown is shorter than the outer side; on M^{4-6} it is rather longer. The posterior border of the crown runs from antero-internal to postero-external, also forming an acute angle with the outer border. This posterior side is longer than the anterior one on M^{1-3}, about the same length on M^{4-5}, and shorter on M^6. Anterior and posterior sides are essentially straight lines, forming shearing edges,

but the external border is bilobed, with a median notch which becomes progressively more marked from M^1 to M^5.

The inner angle of the crown is produced into a high cusp which dominates the tooth, and from its apex descend the anterior and posterior shearing edges. On each of these latter, about halfway between the internal cusp and the external margin, is a small but distinct cusp, that on the posterior edge being the larger of the two. These cusps may be described as semi-conical in shape—the face toward the centre of the tooth is rounded while the other face is formed by the nearly vertical shearing plane which passes through the apex of the cusp. The median part of the crown is basined, with its external border elevated into a sharp cuspidate ridge, but this is not so high as the anterior and posterior margins, nor are its cusps so prominent. The largest of these is antero-external, directly external to the median anterior cusp just described. At the median emargination the external rim is lowest and on the posterior lobe it rises again and becomes obscurely cusp-like. This is made more clear by the accompanying figures. The main, internal cusp is not quite erect, but points somewhat backwards.

The interstices or embrasures between the molars are widely open, very notably so in comparison to such a type as *Kurtodon*, for instance.

The last molar, M^6, is now broken, giving it a very different aspect from the other molars, but it seems to have resembled the latter save for the reduction of the postero-external lobe. It is thus at the same time more transverse and more oblique than the preceding teeth.

Skull.

The maxilla as preserved is very uncharacteristic. There is a small infraorbital foramen above the anterior root of M^3 and apparently another, larger, one above the anterior end of M^2. The zygoma arose at a point just above M^6. The part of the maxilla immediately above the teeth is very flat. The palate is not exposed save anteriorly, where it shows no features of interest.

Measurements.

Maximum lengths in millimetres :

	P^3.	M^1.	M^2.	M^3.	M^4.	M^5.	M^6.	M^{1-6}.
47740	1·6	1·3	1·6	1·8	1·5	1·4	0·6	8·7

Order PANTOTHERIA Marsh.

Diagnosis.—Small Jurassic mammals, incisors not specialized, canines present and often two-fanged, premolars generally piercing and trenchant, never fully molariform and usually very different from the molars. Molars primitively trigonal, interlocking, and to some extent overlapping. The upper molars with one main inner cusp and one main outer cusp (which may be much reduced) and always two or more other cusps variously developed. The lower molars with an asymmetrical trigonid of three

cusps and a talonid which is primitively unbasined, with but one cusp, but which in one specialized group (Dicrocynodontidae) becomes basined and has more than one cusp. Lower molars sometimes with an outer, but never with an inner, cingulum. Primitive cheek-tooth formula apparently P^{1}_{4} . M^{3}_{3}, but sometimes reduced considerably. Mandible unankylosed at symphysis, with internal groove and distinct coronoid, condylar, and angular processes, the latter uninflected. Condyle not transverse, above alveolar level.

Discussion.—One of the original two Mesozoic mammal jaws from Stonesfield was a pantothere, and members of this group outnumber those of any other in Owen's classic monograph (1871), but it was not until 1880, when Marsh defined the order Pantotheria, that the unity of the group was recognized. In his final paper on the order (1887) Professor Marsh specifically included in it the families Dryolestidae, Diplocynodontidae [Dicrocynodontidae], Paurodontidae, and Dromatheriidae. From the characters listed and from his discussion it is obvious that the order was really founded on the first three of these families. It is a moot question whether Marsh intended to include the forms now known as triconodonts and symmetrodonts. He did not specifically so state, and one of the characters of his Pantotheria, *i.e.* "Angle of lower jaw without distinct inflection," would definitely exclude these two groups as understood by him, for he accepted the current view that they showed inflected angular processes. It is therefore probable that triconodonts and symmetrodonts were never intended to be taken as members of the Pantotheria, although no other place for them was suggested.

Osborn (1888a) separated the forms now referred to the Pantotheria into three or four groups of distinct origin, but in the same year (1888b) he corrected the misconceptions on which this disposition rested and pointed out that there were (exclusive of multituberculates) but two main molar types in the English Jurassic, the triconodont type and the tritubercular type. It is of interest that he apparently included the symmetrodonts with the trituberculates at this time, a view which he never again has held. In regard to family classification, in his memoir (1888a) Osborn recognized the families Amphitheriidae, Peralestidae, Kurtodontidae Amblotheriidae, and Stylacodontidae. His grouping of the various genera within those families was based on a number of serious misconceptions of their true molar structure, but those errors were mostly corrected in the same year (1888b) and the families Peralestidae and Kurtodontidae were eliminated.

In his address on the Rise of Mammals in North America (1893) the same eminent authority consistently grouped the pantotheres (minus the triconodonts and symmetrodonts) together and called them tritubercules. Unfortunately, the same word was here used in a morphological and not taxonomic sense for Upper Cretaceous forms, which, as he pointed out, are very distinct from the so-called Jurassic tritubercules. This has given rise to great confusion, it being generally accepted that the Cretaceous forms, too, should be placed in the order Trituberculata, although this was clearly not Osborn's intention. The ordinal name Trituberculata Osborn, by which the pantotheres are now most widely known, was apparently first used in 1893 in the third volume of Zittel's great "Handbuch."

In his final classification (1907) Osborn called the order "Pantotheria Marsh (Trituberculata Osborn)," and included in it the families Amphitheriidae, Amblotheriidae or Stylacodontidae, Paurodontidae, and Diplocynodontidae [Dicrocynodontidae]. Although the grounds on which the families are based are now different and although their contents are somewhat changed, this is essentially the same grouping as that adopted in the present memoir. The chief defect of the classification as given by Osborn lay in the impossibility of gaining an adequate conception of the characters separating the Amphitheriidae from the more advanced family which is here called the Dryolestidae. Gregory (1922) was inevitably led by the erroneous statements in the literature into still further error in this regard, his conception of the distinctive characters of the "Stylodontidae" being at that time entirely incorrect.

The present classification, based on personal knowledge of all the known specimens of pantotheres, divides the order into four families: Amphitheriidae, with only *Amphitherium;* Dryolestidae, with most of the Purbeckian and Morrison pantotheres; Paurodontidae, with rather more primitive molars than the other Upper Jurassic forms; and Dicrocynodontidae, with a small number of aberrant genera.

The ordinal designation Pantotheria, which is here consistently used to the exclusion of any other, has been very widely abandoned for Osborn's designation Trituberculata. The name Pantotheria was proposed in 1880, with the evident but not very explicit significance of "generalized mammal" (*πάς, παντὸς,* all, in general, *θηρίον,* wild beast or mammal). The name Trituberculata was proposed in 1893, with reference to the supposed character of the teeth. Rules of priority do not necessarily apply to ordinal names. The use of "Pantotheria" has been objected to on the grounds that it is either invalid or seriously objectionable, and were this true and were not "Trituberculata" much more objectionable, one could only reasonably adopt the latter, which is widely in use at present.

The only reason for rejecting Pantotheria on grounds of validity lies in the supposed fact that it included triconodonts and symmetrodonts as well as true pantotheres. As pointed out above, it is by no means certain that Marsh really meant to include these extraneous groups, and even if he did, the order was founded not on them but on forms entirely distinctive of the natural order. Few ordinal designations now in use would be valid if the removal of some animals from the group made a new name for it necessary. The only other objection to the name Pantotheria is formal, it being held that names ending in "-theria" should be reserved for the major groups of mammals, such as the Prototheria, Metatheria, and Eutheria. This objection is at least supermeticulous. The termination -theria has been used, and misused, in the freest manner for groups large and small, hypothetical and real, in senses taxonomic, morphological, or philosophical. There is no fixed usage in this respect. Even if there were, the name would not be entirely inappropriate, for it will be shown below that the Pantotheria cannot be definitely referred either to the Eutheria or to the Metatheria, although undoubtedly related in some way to both.

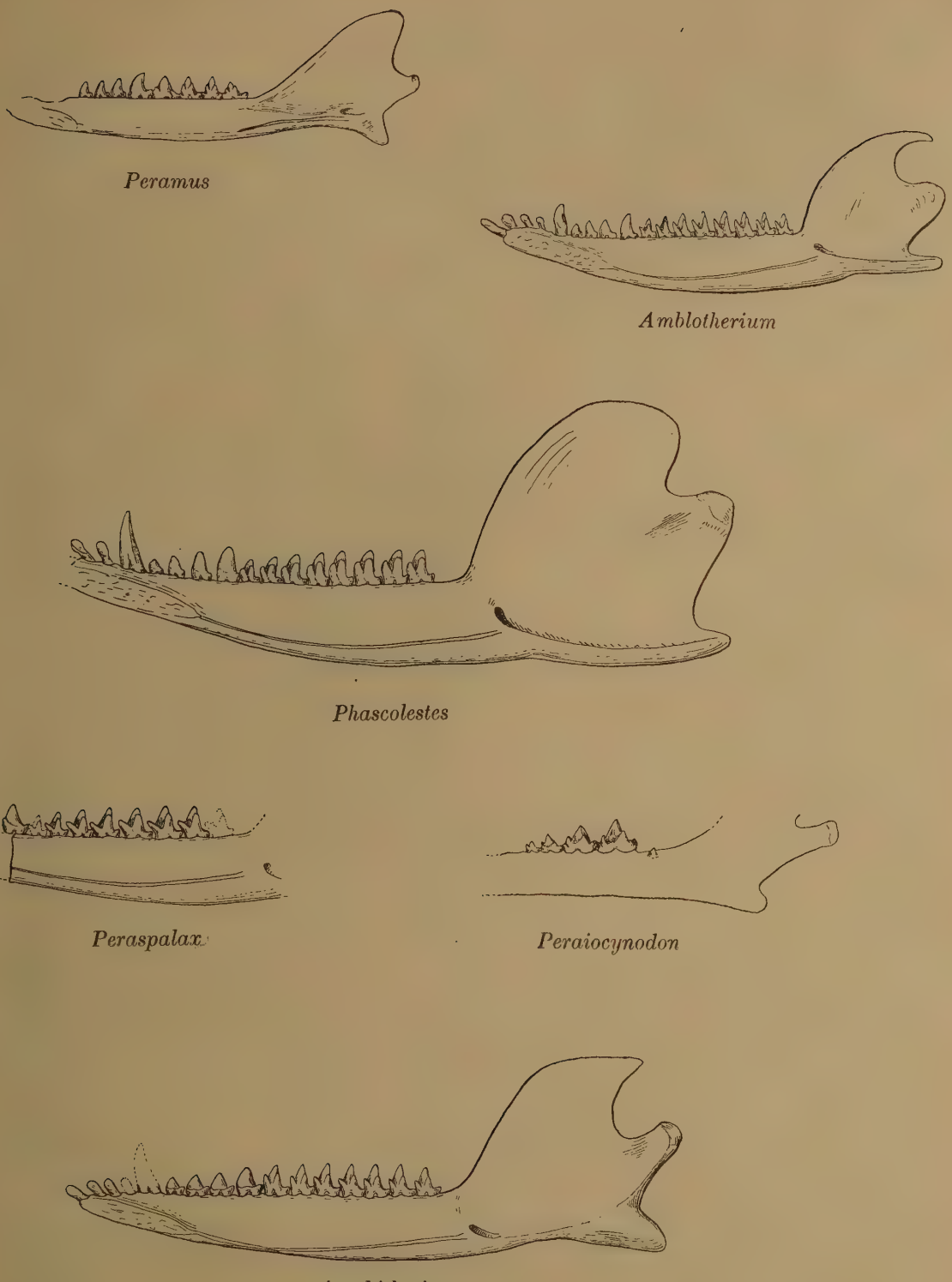


FIG. 35.—Comparative internal views of right mandibular rami of the known European genera of Pantotheria. All × 4 diam.

The prior term Pantotheria thus is valid and acceptable. The term Trituberculata is objectionable on two counts at least. In the first place, the word "tritubercular" is a morphological term in wide use and applied to the teeth of many orders. Thus the Upper Cretaceous tritubercular teeth certainly do not belong to the order Trituberculata Osborn, although the identity in terms has led to the most regrettable misunderstanding in this respect and will continue to do so if they are still used. In the second place, although there are many teeth which are properly called tritubercular, those of the so-called "Trituberculata" are not. This again has naturally led to confusion, which can be avoided only by abandoning the name Trituberculata in favour of the prior and less misleading Pantotheria.

Pantotherian Evolution.

Pantotheres are known as such from only two horizons—the Stonesfield, Middle Jurassic, and the Purbeck and Morrison, Uppermost Jurassic. From the earlier horizon but a single genus is known. Very fortunately, however, one may be fairly certain that this genus, *Amphitherium*, is a fair sample of pantotherian life at the time. It is primitive in every respect and forms an ideal ancestor for the later and more specialized forms, as its morphology will show.

The Purbeck-Morrison genera fall into three definite groups, here defined as families, each of which is specializing in its own peculiar way on the basis of an essentially *Amphitherium*-like ancestry. Of all of these genera, *Peramus* is the most primitive. Essentially its molars differ from those of *Amphitherium* only in the rather narrower heel and the addition of a tiny antero-internal basal cusp. The group to which it is referred, the origin of which it goes far to elucidate, is the family Paurodontidae. In this family the primitive *Amphitherium* type of molar is retained almost unchanged, while the number of cheek teeth tends to be reduced and the jaw to shorten. The importance of this will be more fully alluded to in discussing the affinities of the order as a whole, but it may be pointed out here that this retention of the most primitive type of tuberculo-sectorial molar, accompanied by a reduction in the number of molars to four, is exactly what must have occurred in the ancestry of both the marsupials and placentals. In the Paurodontidae reduction went much farther, it is true, for once started in a path of specialization there is not infrequently seen a strong tendency to continue in this path, even to extremes. The most extreme instance in the present case is that of *Paurodon* and *Archaeotrigon* which have $P_2 \,.\, M_4$, or perhaps even only $P_2 \,.\, M_3$ in some cases. This is the smallest number of cheek teeth known in any pantothere.

The next group, and by far the largest one known, is that of the Dryolestidae, including all the well-known Purbeck and Morrison genera. Many serious misconceptions have been and still are entertained as to the characters of these genera, and this fact has led at times to their wide separation. As it happens, they are very similar indeed, and form a small closed group of closely related genera, differing only in minor points of dental structure. When these are compared with the *Amphitherium* type, which is without doubt structurally ancestral to them, it is seen that the tooth

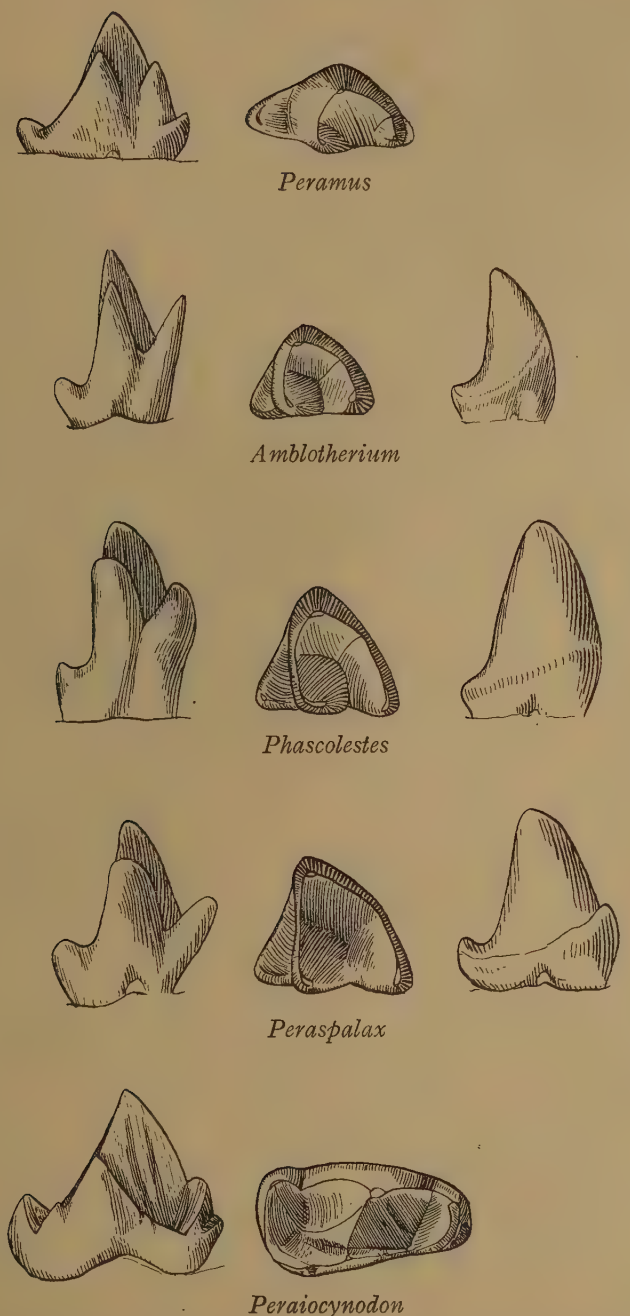
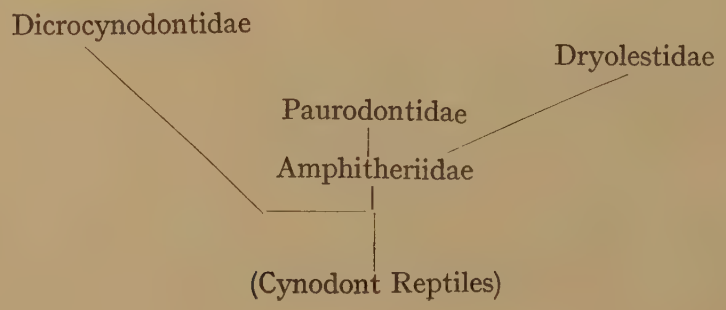


FIG. 36.—Comparative views of left cheek teeth of European Upper Jurassic Pantotheria. To the left, internal aspects of typical molars. In middle, crown views of same. To the right, internal views of last premolars. All × 20 diam.

series has, as it were, been crowded together longitudinally, so that the trigonids are compressed antero-posteriorly and the talonids are reduced. This reduction of the talonids has an interesting and invariable index in the character of the roots, the posterior root becoming in this family very small and being confined to the internal side of the crown. At the same time that these changes were taking place the trigonid became basined by the upgrowth of its sides, and especially by the specialization of the paraconid and more particularly of the metaconid, which may become quite as high as the protoconid. Discussion of the little we know of the concomitant specialization of the upper dentition is reserved for another place, the evidence being chiefly extra-European; here it will only be said that what seems to have occurred was a progressive antero-posterior shortening of the crown with increasing emphasis on its internal angle, the external cusps eventually becoming almost insignificant in size. The English dryolestid upper molars so far known seem to belong to the most specialized type. The dryolestids were advancing along lines of their own and one cannot hold them to have been either directly or structurally ancestral to any later mammals, although of course they are extremely primitive and cast much light on the Upper Jurassic grade of mammalian structure.

The last Upper Jurassic group is that of the Dicrocynodontidae, a most extraordinary family, in which the teeth are highly complicated, with furrowed cusps, new cusps not otherwise known in pantotheres, basined talonids, and other unusual characters. At first sight it is difficult to believe that these creatures can really be closely related to the other pantotheres, but a more detailed examination shows that this is indeed the case. Their teeth have the same cusps and the same occlusal relationships, but they are superficially complicated by the addition of a number of new characters without the real loss of any of the older ones. They are even more aberrant than the dryolestids, but it is a rapid and premature specialization which made them so, and not a profound one. The union of their ancestral line with that of the other known pantotheres would, perhaps, have to be sought at a stage somewhat more primitive than that represented by *Amphitherium*.

A detailed discussion of the still more important question of pantotherian relationships to contemporary and later orders is deferred to a later page, when their morphology shall have been set forth and all can be discussed. The apparent relationships of the various pantotherian families may be roughly represented by the following scheme:



Synonymy.

In order to facilitate an understanding of the rather difficult synonymy of the Symmetrodonta and Pantotheria, the names used for the English species in the four revisions of the groups are given below.

Of the fifteen species given by Owen in 1871 only three have been accepted unchanged in the other works, and only four are here recognized as valid in the original form. These many changes are due neither to any deficiency on Owen's part nor to a hypercritical attitude on the part of later students, but entirely to the difficulties inherent in the subject and insuperable in 1871.

Owen, 1871.	Lydekker, 1887.	Osborn, 1888a–1888b.	This Memoir.
Spalacotherium tricuspidens. S. minus.	Spalacotherium tricuspidens. S. minus.	Spalacotherium tricuspidens. (Omitted) Peramus minus.	Spalacotherium tricuspidens. Peramus tenuirostris.
Amblotherium soricinum. A. mustelula.	Amblotherium soricinum. A. mustelula.	Amblotherium soricinum. (Omitted.)	Amblotherium pusillum. Phascolestes mustelula.
Peralestes longirostris.	Peralestes longirostris.	Peralestes longirostris.	Peralestes longirostris.
Phascolestes ? longirostris. P. dubius.	Amblotherium mustelula. (Omitted.)	Phascolestes dubius. (Omitted.)	Phascolestes mustelula. (Nomen nudum.)
Achyrodon nanus. A. pusillus.	Achyrodon nanus. A. pusillus.	Achyrodon nanus. (Omitted.)	Amblotherium nanum. Amblotherium pusillum.
Peraspalax talpoides.	Amblotherium talpoides.	Peraspalax talpoides.	Peraspalax talpoides.
Peramus tenuirostris. P. minor ?	Peramus tenuirostris. P. tenuirostris ?	Peramus tenuirostris. (Omitted) Peramus minor.	Peramus tenuirostris. P. tenuirostris.
Stylodon pusillus. S. robustus. S. pusillus (pars).	Stylodon pusillus. S. robustus. S. pusillus.	Stylodon pusillus. (Omitted.) Kurtodon pusillus.	Amblotherium pusillum. Amb. pusillum. Kurtodon pusillus.
Leptocladus ? dubius ?	Leptocladus dubius.	Leptocladus dubius. Peramus dubius.	Peramus tenuirostris.

Family AMPHITHERIIDAE Owen.

Diagnosis.—Pantotheria with lower molars with four cusps only. Heel fairly long but not basined, with a single cusp more posterior than purely internal in position. Crown supported by two stout subequal roots. Cheek teeth eleven (or possibly twelve) in number. Jaw slender and long.

Discussion.—This family has at times been made to include a variety of distantly related, or even unrelated, forms. Thus in Osborn (1888a) it includes *Amphitherium*, the dicrocynodontids and *Peramus*. Lydekker (1887) included *Phascolotherium*, *Amphilestes*, *Amphitherium*, and such of the Purbeckian pantotheres as were based on specimens seen in internal aspect. In Osborn's last classification (1907) it includes *Amphitherium*, *Amphitylus*, and *Peramus*, with *Leptocladus*, this being the first time that a truly natural group was obtained. In the present memoir the genus *Amphitylus* is not recognized, while *Peramus* is transferred to the Paurodontidae, but the grouping given by Osborn is quite tenable in the light of later research. Gregory (1922) makes an unnatural division of the

dryolestids and refers some of them to the Amphitheriidae. *Paurodon* and *Peralestes* are doubtfully referred by him to this family.

The characters which distinguish *Amphitherium* from the Upper Jurassic pantotheres are primitive features. *Amphitherium* does not show any of the diverse specializations that mark all its later relatives or descendants. For this reason it seems most practical to retain it alone in the family Amphitheriidae, which may be considered as *structurally* ancestral to all later pantotheres, and indeed in a broad sense probably also to all marsupials and placentals. The family and the genus on which it is based are thus perhaps the most interesting and important of those known from the Mesozoic.

Genus AMPHITHERIUM Blainville, 1838.

(Text-fig. 35.)

1838. *Amphitherium* Blainville, *C. R. Acad. Sci.*, Paris, VII, p. 417.
1838. *Heterotherium* Blainville, *C. R. Acad. Sci.*, Paris, VII, p. 417.
1838. *Amphigonus* Agassiz, in Buckland, *Geologie in Mineralogie*, trans. by Agassiz, II, p. 3.
1838. *Thylacotherium* Valenciennes, *C. R. Acad. Sci.*, Paris, VII, p. 580.
1838. *Botheration-therium* Charlesworth, *Athenaeum*, 6 Oct. 1838, p. 731. [*Nom. fictum.*]
1838. *Botheratiotherium* Blainville, *C. R. Acad. Sci.*, Paris, VII, p. 735. [For *Botheration-therium.*]

Diagnosis.—With the characters of the family.
Genotype.—*A. prevostii* (H. v. Meyer).

Amphitherium prevostii (H. v. Meyer).

(Pl. VIII, fig. 1 ; Text-figs. 37–38.)

1832. *Didelphis* (?) *prevostii* H. v. Meyer, *Palaeologica*, p. 55.
1838. *Didelphis prevostii* Blainville, *C. R. Acad. Sci.*, Paris, VII, p. 403.
1838. *Thylacotherium prevostii* Valenciennes, *C. R. Acad. Sci.*, Paris, VII, p. 580
1845. *Amphitherium prevostii* Owen, " Odontography," p. 377.
1888. *Amphitylus oweni* Osborn, *Jour. Acad. Nat. Sci.*, Philadelphia, IX, p. 192.
1894. *Amphitherium oweni* Goodrich, *Quart. Jour. Micr. Sci.*, XXXV, p. 9.

Diagnosis.—(The only species of the genus.)
Formation and Locality.—Stonesfield slate, Stonesfield, Oxfordshire.
Material.—(*a*) In the British Museum :

36822. Part of right ramus, internal aspect, with P_4 and M_{1-5}. Figd., Osborn, 1888A, fig. 2 ; Goodrich, 1894, pl. xvi. fig. 4. (*Morris Colln., Purchased* 1862.)
M 2298. Cast of Oxford Specimen I. (*Presented by Prof. Prestwich,* 1884.)
M 2299. Cast of Oxford Specimen II. (*Same history.*)
M 5967. Model, enlarged eight times, of Oxford Specimen I., made by W. P. Pycraft. (*Presented by Sir E. Ray Lankester.*)

M 5969. Model, enlarged eight times, of Oxford Specimen II, made by W. P. Pycraft. (*Same history.*)

(*b*) In the University Museum, Oxford :

I. Left ramus, internal aspect, with P_{1-4} and M_{1-6}, mostly badly broken. This is the holotype, and was the first Mesozoic mammal to be made known. Figd., Prevost, 1825, pl. xviii, fig. 2 ; Buckland, 1837, pl. ii, fig. B ; Owen, 1841, pl. v, fig. 3, 1846, fig. 16, 1871, pl. i, fig. 21 ; Goodrich, 1894, pl. xxvi, fig. 1 ; and elsewhere.

II. Right ramus in external aspect, with I_{1-3}, base of canine, and bases or broken crowns of all premolars and molars. Holotype, *Amphitylus oweni* Osborn. Figd., Owen, 1845, pl. xcix, fig. 1, 1846, fig. 15, 1871, pl. i, fig. 23 ; Goodrich, 1894, pl. xxvi, fig. 3.

III. Left ramus, internal aspect, with P_{3-4}, M_{6-7}, and much of the mandible preserved. Figd., Owen, 1841, pl. v, fig. 1, 1871, pl. i, fig. 22 ; Goodrich, 1894, pl. xxvi, fig. 2.

Dentition.

Dental Formula.—Owen gave the cheek-tooth formula as P_6, M_6, but Lydekker suggested P_4, M_7 for Oxford II. Osborn (1888A, pp. 228, 231) adopted the latter formula for that specimen, which he believed to represent a new genus, but gave the formula $P_4 . M_6$ for *Amphitherium* proper. He later (1888B, pp. 295, 297) gave " either $P_5 . M_6$ or $P_4 . M_7$ " for the second Oxford specimen, and definitely proposed $P_5 . M_6$ for *Amphitherium*. Goodrich (1894, p. 11) also adopted the formula $P_5 . M_6$. Since the second Oxford specimen clearly has eleven cheek teeth, not divisible in their broken condition, while the first Oxford specimen certainly shows but six molars, it would seem to follow that there must be five premolars. Nevertheless, this conclusion is incorrect. In the first Oxford specimen the length of M_{1-6} is 7·0 mm. In the third Oxford specimen the distance from the posterior end of the last preserved premolar (which comparison with the first specimen clearly proves to be the last indeed) to the posterior end of the one preserved complete molar is 7·1 mm. Clearly this molar in this specimen is the sixth and not the fifth, as supposed by Goodrich. Behind it, as first discovered by Osborn, is another, seventh, molar just beginning to appear. In the second Oxford specimen, which other evidence also indicates as the oldest of the three, we may conclude that all seven molars are in place. There can thus be only four premolars, a number which is never exceeded in early mammals (save multituberculates), so far as known. In the third Oxford specimen, which was apparently better preserved in his day than in ours, Owen believed there to be six alveoli in front of the teeth preserved, *i.e.* one socket each for three incisors and a canine, and two for P_1. It seems quite certain, however, that the first four were incisive alveoli, and that the last two were for the canine, which is shown by the second Oxford specimen to be two-rooted. The first tooth of which the base is preserved is the first premolar. The most probable formula, as shown by the material, is thus $I_4 . C_1 . P_4 . M_7$. It is by no means impossible

that an eighth molar appeared still later in life. Indeed, this may be probable in view of the fact that many of the later and less primitive genera of pantotheres have eight molars, of which the last sometimes appears only relatively late in life.

Incisors.—The first three incisors are present in the second Oxford specimen, but they are rather indifferently preserved. They are small, styloid, semi-procumbent, and are arranged in an antero-posterior series, but with the first one slightly internal. They are not crowded, but there are no distinct diastemata. I_4 is represented only by its alveolus.

Canine.—The crown of the canine is unknown, but its base and roots are seen in the second Oxford specimen. It is large, only a little compressed laterally, and is slightly more external anteriorly than posteriorly. There is a distinct vertical median basal groove, indicating a division of the fang within the alveolus, but the two stout roots apparently were little divergent. The canine is slightly procumbent.

Premolars.—The four premolars increase progressively in size. The last does not overtop the first molar as in most pantotheres, being somewhat lower than the protoconid of the latter. Each premolar consists of a single transversely compressed, somewhat recurved, trenchant main cusp with a posterior cuspidate cingulur heel of moderate development. There is a sharp continuous internal cingulum which rises centrally and also anteriorly, where it passes into the anterior border. There is a slight break in the even contour of the tooth here but no true anterior cusp. The apparent postero-internal cusp seen in the third Oxford specimen and suggested by Goodrich possibly to be a deuterocone is more probably part of the posterior cusp which has become isolated and accentuated by wear or breakage.

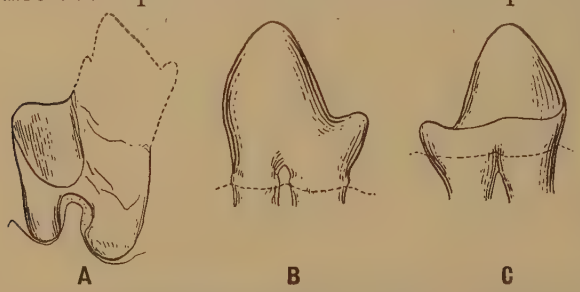


Fig. 37.—*Amphitherium prevostii* (v. Meyer). A, external view of broken right lower molar with worn heel. B, external view of left P_4. C, internal view of left P_4. All × 20 diam.

Molars.—The seven known molars appear to be of the same size and structure. This structure can now be made out in its entirety, by the addition of the few details necessarily lacking in Professor Goodrich's accurate and lucid description (1894, pp. 8–9, figs. 1, 2). The molar is of the most primitive tuberculo-sectorial type known. The trigonid has only the three primitive cusps, protoconid, paraconid, and metaconid. The former is markedly the highest and dominates the tooth. Its external surface is convex, and it is probable that there was no external cingulum. As seen from the inside its anterior contour is somewhat convex, its posterior one straight and more nearly vertical. This cusp is connected to the paraconid and metaconid by shearing edges, one to each. These two internal trigonid cusps are of very nearly the same height, with the pa^d even a little the higher on the anterior molars and but little lower on the more posterior ones. The trigonid is not symmetrical, the me^d being more nearly directly internal to the pr^d than is the pa^d, although the

pr^d–me^d crest is not quite transverse. There is no trigonid basin, as no ridge or crest, however small, unites the bases of the pa^d and me^d.

Although much smaller than the trigonid, the talonid is relatively somewhat larger than in most of the Upper Jurassic pantotheres, and it rises into a very distinct cusp, with its apex directly in the median longitudinal axis of the tooth. This cusp corresponds here in position to the hypoconulid of Tertiary mammals. On the other hand, it is certainly homologous with the dryolestid talonid cusp, and the latter occupies the position of an entoconid. It is probable that this cusp, even when postero-median rather than postero-internal, is an entoconid homologically, but this will not be certain until more Cretaceous material is available to fill the gap between the basinless pantothere heel and the basined insectivore or didelphid type. In *Amphitherium* (and indeed in most pantotheres) this cusp is connected by a ridge to the postero-internal angle of the base of the trigonid. There is no other cusp and no corresponding external ridge, hence the heel is quite unbasined. Instead, as will be more clearly understood from the figures (fig. 38), the shelf-like heel

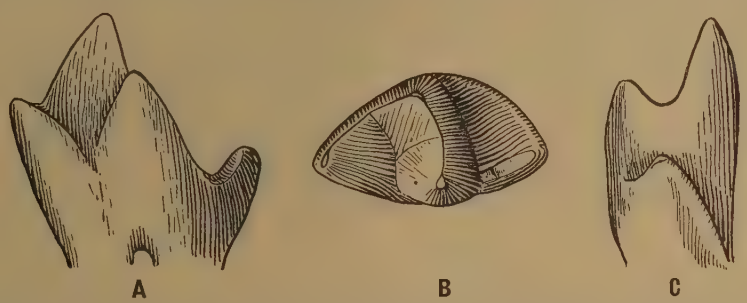


FIG. 38.—*Amphitherium prevostii* (v. Meyer). Right lower M_5 of B.M. 36822. A, internal view. B, crown view. C, posterior view. All × 30 diam. Upper Jurassic, middle Purbeck beds, Swanage, Dorsetshire.

narrows and sinks to a lower level rapidly on passing externally, disappearing at the postero-external angle of the base of the trigonid. The structure thus described differs from that previously assigned to *Amphitherium* and also differs in details from theoretical reconstructions of the most primitive tuberculo-sectorial molar, but every point included in the above description can be verified by reference to the originals, involving no reconstruction or conjecture.

In the second Oxford specimen, which is the oldest individual in the collections, the heel is worn and there is a rounded groove running straight externally and downward from the notch between the talonid cusp and metaconid. This oblique groove clearly marks the path of the protocone in the last stages of the shearing and grasping bite, and has an important bearing on molar evolution, which I hope to point out in more detail elsewhere.

Each molar is implanted by two stout roots. These are nearly or quite equal in size, although in the posterior molars the posterior root does not extend quite so far externally as does the anterior one. As noted by Goodrich, the roots are slightly swollen just above the alveoli externally.

Mandible.

The alveolar border is long and straight. The lower border forms a long sweeping curve, which is continued back to the condyle internally by the low ridge which runs from the latter forward to a point below the dental foramen. The angular process projects sharply backward and downward at a point about halfway between the condyle and dental foramen. The external face of this process is somewhat concave, the internal somewhat convex. If a line is drawn from the apex of the coronoid to the end of the angle it passes through the condyle—that is to say, the angle is not at all inflected. The articular condyle is elevated well above the molar level. From it externally there runs downward and forward a thickening or buttress into, but not across, the masseteric fossa. The coronoid is high and stout, ending in a sharp, but not acute, backwardly directed point. The masseteric fossa is deep and strongly defined. The dental foramen has its primitive position at the anterior end of the pterygoid fossa below the anterior end of the coronoid. Just anterior to it begins the internal groove, which curves forward, almost reaching the lower border beneath the posterior premolars, but then turning slightly upward and passing into the posterior end of the symphysial surface. The latter is long and low, and ends beneath P_1.

In the second Oxford specimen there are four mental foramina: a small one below I_3, one of equal size below I_4, a larger and higher one between C and P_1, and a still larger and higher one below P_3.

Measurements.

	C.	P_1.	P_2.	P_3.	P_4.	P_{1-4}.	M_1.	M_2.	M_3.	M_4.	M_5.	M_6.	M_{1-6}.
Oxford I	—	0·75	0·9	1·0	1·2	4·1	—	—	—	1·2	—	—	7·0
Oxford II	0·9	0·8	0·8	0·9	1·1	3·8	—	—	—	—	—	—	6·8
Oxford III	—	—	—	1·0	1·2	—	—	—	—	—	—	1·0	7·1
36822..	—	—	—	—	0·8	—	0·9	0·9	0·9	1·0	1·1	—	—

	Depth below M_4 inside.	Posterior end M_6 to condyle.	Vertical-coronoid to angle.
Oxford I	2·6	8·0	7·6
Oxford II	—	11·0	8·3
Oxford III	2·8	8·8	—
36822..	2·0	—	—

Taxonomy and Nomenclature.

The first name applied to this genus was *Heterotherium* (Blainville, 1838, p. 417). "Il est plus certain que cet animal doit former un genre distinct auquel on pourrait donner le nom de *Heterotherium* ou d'*Amphitherium* . . ." The specific name *Didelphis prevostii* had been used for the first time by H. v. Meyer in 1832. It is credited to Cuvier, but is apparently *ex MS.*, so that it is actually von Meyer's name. Although the combinations *Heterotherium prevostii* or *Amphitherium prevostii* do not occur in Blainville, it is clearly indicated that the type of these alternative genera is *Didelphis prevostii*. On this basis *Heterotherium* would be the valid name

(a fact hitherto overlooked), but fortunately it proves to be pre-occupied by *Heterotherium* Fischer de Waldheim, 1822, so that *Amphitherium* is the correct generic designation. *Amphigonus* Agassiz has been supposed (as in Owen, 1871, p. 12) to have been proposed in 1835, but Agassiz's note of that date does not mention this name, and it was not formally proposed until 1838, probably (but not certainly) after de Blainville's publication. Valenciennes proposed the name *Thylacotherium* in 1838, but at a later date than the publication of *Amphitherium*. The only excuse which he gives for setting aside the three terms already given to the fossil is that they all express a certain doubt concerning its affinities—a doubt which he professes not to share. The name is invalid, of course. In the same year, writing in the *Athenaeum*, Charlesworth avoided taking sides in the nomenclatorial battle by using the name *Botheration-therium*, a suggestion taken quite seriously by Blainville at whose hands it became *Botheratiotherium*.

Osborn (1888A) later established a new but related genus, *Amphitylus*, based on the second Oxford specimen. As Goodrich has pointed out (1894, p. 10), it is certain that this jaw is congeneric with the type of *Amphitherium*. Goodrich upholds its specific separation as *Amphitherium oweni* (Osborn) on the following grounds:

1. The coronoid is straight above and more pointed posteriorly.
2. The condyle is more slender and the supracondylar notch more pronounced.
3. The angle is larger and produced farther back.
4. The cusps of P_3 are more rounded, the main cusp farther forward and the swelling of the fangs strongly developed.

To these may be added:

5. The premolars are very slightly larger.
6. The postmolar part of the jaw is larger in every dimension.

1 and 3 are slight differences and could well be due to the known fact (brought out below) that this individual is older than the type. 6 is certainly due to this cause. The apparent differences in P_3 are due in large part to its being seen in external aspect, whereas all the other specimens show the premolars in internal aspect. Finally, the difference in premolar size is only 7 or 8 per cent. at most—certainly within the range of intra-specific variation. In short, there appears to be no definite specific distinction between this jaw and the first Oxford specimen, and *Amphitylus oweni* must be considered a synonym of *Amphitherium prevostii*.

The three Oxford specimens represent three distinct ages in the life of *Amphitherium prevostii*. The type is the youngest, with no trace of M_7 and with a slender ramus and relatively very small postmolar region. The third specimen is next in age, with M_7 just appearing, and the mandible intermediate in size. The second specimen is the oldest yet known, with M_7 in full use and the mandible stout and large, its morphology well defined. The British Museum specimen (36822) is perhaps younger than any other, as its horizontal ramus seems to be unusually slender, but the bone is too poorly preserved for definite pronouncement.

Family PAURODONTIDAE Marsh.

Diagnosis.—Pantotheria with trigonid elongate, not compressed antero-posteriorly, me^d markedly lower than pr^d. Talonid not reduced, semicircular or triangular in plan, with one cusp, posterior or postero-internal in position. Lower molars supported by two large subequal roots. Cheek teeth reduced in number. Lower jaw usually short and stout.

Discussion.—This family was founded by Marsh (1887, p. 341) for the single genus *Paurodon*. Its distinctive features have saved it from much taxonomic wandering, although Osborn (1888A, but not 1907) and Gregory (1922) have referred it to the Amphitheriidae, the latter noting that its reference to a distinctive family would depend on confirmation of Marsh's description. It has been possible to confirm Marsh's work in the points questioned, and to redefine the family, adding two new members (Simpson, 1927). The group now includes *Paurodon*, *Archaeotrigon*, and *Tathiodon* from the American Morrison; *Peramus*, from the Purbeckian, although rather different, is best also placed here.

In their molar structure the paurodontids are unquestionably the most primitive of Upper Jurassic pantotheres. They do not show the shortening of the heel, the compression of the trigonid, or the upgrowth and specialization of the metaconid so characteristic of the dryolestids, nor do they suggest the extraordinary elaboration of the dicrocynodontids. Their molars are close variants of the primitive *Amphitherium*-type. The derivation of any paurodontid molar from that of *Amphitherium* would involve slight changes in the form of the heel and in the development of the pa^d and me^d (as well as the development of a new cuspule in *Peramus*)—changes quite insignificant in comparison with those required to fashion a dicrocynodontid or even a dryolestid molar from the structurally ancestral *Amphitherium*.

Although such a conclusion could be, and was (Simpson, 1925C, fig. 1D), drawn from the American forms, it remained very tentative as applied only to them, in view of the fact that they seem obviously specialized in the very reduced dental formula and short stout jaw. A suspicion legitimately remained that the apparently primitive molars owed some of their characters to this numerical specialization. *Peramus*, however, tends largely to remove these suspicions. Its dental formula (P_4 . M_4, probably) is less reduced, its lower jaw longer and more *Amphitherium*-like. In dental formula and in form of jaw (as seen not only in the horizontal ramus but also in the angular process) *Peramus* thus tends to bridge over the gap between the Paurodontidae and the Amphitheriidae, while showing, of course, certain aberrant features of its own the most striking of which is the presence of an antero-internal accessory cusp, elsewhere known among Pantotheria only among dicrocynodontids, where it was probably independently acquired.

It does not seem necessary, or possible, on this evidence to unite the two families Amphitheriidae and Paurodontidae, which are still strikingly different in their typical development. There is some question, however, as to which family should properly receive the genus *Peramus*. It seems preferable to place it in the

Paurodontidae, but reference to the Amphitheriidae would perhaps be equally defensible and would involve no different interpretation of the facts.

Genus PERAMUS Owen 1871.

(Text-figs. 35–36.)

1871. *Peramus* Owen, " Fos. Mam. Mesozoic," p. 41.

1871. *Leptocladus* Owen, " Fos. Mam. Mesozoic," p. 53.

Diagnosis.—Paurodontidae with trigonid with distinct pointed pa^d and me^d, the latter higher, but the pr^d distinctly higher than either, and with a very small antero-internal basal cuspule. Heel elongated, with a distinct postero-median cusp. Dental formula probably $P_4 \,.\, M_4$. Horizontal ramus slender.

Discussion.—Besides the genotype, *Peramus tenuirostris*, Owen tentatively referred a species *P. minor* to this genus, but the differences between them do not appear to be sufficient to validate specific distinction. *Spalacotherium minus* also proves to belong to this genus, but it too is probably conspecific with the genotype so that only *Peramus tenuirostris* is recognized.

Peramus tenuirostris Owen.

(Pl. VIII, figs. 2–6.)

1871. *Peramus tenuirostris* Owen, " Fos. Mam. Mesozoic," p. 41.

1871. *Peramus minor* Owen, " Fos. Mam. Mesozoic," p. 44.

1871. *Leptocladus dubius* Owen, " Fos. Mam. Mesozoic," p. 53.

1871. *Spalacotherium minus* Owen, " Fos. Mam. Mesozoic," p. 28.

1888. *Peramus dubius* Osborn, *Jour. Acad. Nat. Sci.*, Philadelphia, IX, p. 295.

1888. *Peramus minus* [*sic*] Osborn, *Proc. Acad. Nat. Sci.*, Philadelphia, 1888, p. 295.

Diagnosis.—The only species of the genus. Length of last three molars about 3·3 mm., or slightly less.

Formation and Locality.—Purbeckian of Durdlestone Bay, Swanage, Dorset.

Material.—All the known specimens are in the British Museum, and form part of the Beckles Colln. (*Purchased in* 1876.)

47742. Left ramus, external aspect, posterior part almost complete, with crowns of last four teeth and roots of several in front of these. Holotype. Figd., Owen, 1871, pl. ii, fig. 10. The basis of the posterior part of Osborn, 1888A, pl. viii, fig. 6.

47739. Left ramus, external aspect, with all the premolars and molars. Holotype of *Leptocladus dubius*. Figd., Owen, 1871, pl. iii, fig. 4; Osborn, 1888A, pl. ix, fig. 10, and 1888B, fig. 1*b*.

47744. Left ramus, external aspect, with first six cheek teeth. Figd., Owen, 1871, pl. ii, fig. 12; Basis of the anterior part of Osborn, 1888A, pl. viii, fig. 6, and figured alone in Osborn, 1888B, fig. 1*c*.

47751. Left ramus internal aspect, with the fourth to sixth cheek teeth. Holotype of *Spalacotherium minus*. Figd., Owen, 1871, pl. i, fig. 39; Osborn, 1888B, fig. 1*a*.

47754. Left ramus, internal aspect, with two broken cheek teeth. Holotype of *Peramus minor*. Figd., Owen, 1871, pl. ii, fig. 13.

47799. Right ramus, internal aspect, with angle complete, and with last two molars, badly broken.

48404. Right ramus, internal aspect, with last three molars.

Dentition.

Dental Formula.—Owen does not give a definite formula for *Peramus*. In one place he speaks of six premolars, in another of seven molars—some teeth obviously having been counted in both series. For *Leptocladus* he suggests, but does not specify, a formula of $P_4 \,.\, M_{4 \text{ or } 5}$. In his large memoir (1888A) Osborn gave the formula as $P_6 \,.\, M_3$, but added a note saying that the almost universal presence of not more than four premolars suggests that this should be $P_4 \,.\, M_5$. In 1888B, however, he definitely supported the formula $I_3 \,.\, C_1 \,.\, P_6 \,.\, M_3$. None of these formulae seems to be correct. The anterior part of the dentition was supposed to be known from 47743, a specimen which actually belongs to an entirely different family (Dryolestidae). The incisor number is quite unknown, these teeth being represented only by a small fragment of one tooth in 47744. The canine is unknown, but it was present. The entire post-canine series is seen in 47739, and consists of only eight teeth. Close comparison of all the other specimens with this one leaves no doubt that eight is the definitive number. The first four are clearly premolars, and the last three are just as clearly molars, but the fifth tooth is doubtful. Osborn wished to refer this tooth, which he called P_6, to the molar series, but was prevented from doing so by its morphology. This tooth is neither molariform nor premolariform. It has a molar-like heel, protoconid, and anterior basal cusp, but it resembles the premolars in the apparent absence of pa^d and me^d. Its reference to either series is equally inconvenient from a morphological point of view. Examination and comparison, especially of specimens 47739, 47742, and 47744, however, bring out certain facts which seem to solve the problem. As is usually the case in mammals, the premolars and the molars are seen to form two separate series as regards degree of protrusion (best studied by noting the point of root-division)—this fact depending on their different times of eruption. The fifth cheek-tooth very definitely falls in with the molar series and differs from the premolar series in this respect. We therefore designate it as M_1 and give the formula as $I_{\frac{1}{1}} \,.\, C_1 \,.\, P_4 \,.\, M_4$. This formula is of the greatest interest and outstanding importance, for it is the only known occurrence of the cheek-tooth formula that must be considered ancestral for both placentals and marsupials. This takes on added significance when one recalls that *Peramus* is the most generalized of Purbeck pantotheres in its molar structure.

Premolars.—The four premolars are of a general type now quite familiar, but they are quite individual in detail. They increase in size and height from before backwards and each consists of a piercing, somewhat laterally compressed, recurved

main cusp, with a small posterior heel rising into a minute cuspule. There is no accessory cusp above this heel. Anteriorly there is, in external aspect, only a faint and rounded suggestion of a tiny cingulum cusp. The internal aspect of these teeth is not exposed on any of the known specimens.

Molars.—The peculiar character of the tooth here determined as M_1 has already been alluded to. In external aspect it seems to fall very readily into the molar series (see especially 47739) for it has the small anterior basal cusp, much more definite than in the premolars and even rather larger than in the succeeding molars and a molar-like heel (although it is true that the difference from that of the premolars is not great), while the main cusp is erect, not recurved, and is rounded in the same way as the molar pr^d and differently from the premolar main cusp. In crown or internal aspect, however, the tooth appears quite unlike the succeeding ones, for there appears to be no development of the internal cusps, the pa^d and me^d. It is hardly possible that these cusps have been removed by wear or breakage in each of the several cases where they should be visible, and there is no alternative but to regard them as very minute or definitely absent, remarkable as this is for a tooth which seems positively to belong to the molar series. It is possible that the anterior basal cusp of this tooth is really the pa^d, but the me^d is lacking in any case.

The last three teeth are definitely molariform. Each is elongated and has five distinct cusps. The pr^d is far the largest of all and is sharp, but not very slender. From its inner side spring the pa^d and me^d. On the posterior molar the me^d is considerably larger and higher than the pa^d, while on the two preceding ones it is slightly larger but of about the same height. Both are erect and sharp, and both are very small relative to the pr^d. They do not seem to rise from a common base with the latter, as in the dryolestids, but rather they spring from the lower slope of the pr^d. Another difference from the dryolestids lies in the absence of a trigonid basin of any sort. The heel also is distinctive: although narrow transversely, it is long and its single cusp is not postero-internal but postero-median. This cusp cannot be seen on M_{2-3} in internal view because the crowded nature of the series and its median position result in its being external to the anterior heel and the base of the pa^d. The anterior heel is another peculiar feature, seen elsewhere only in the aberrant dicrocynodontids. It is at about the same height from the alveoli as the true talonid, but is very small and is confined to the antero-internal angle of the base of the paraconid.

M_{2-3} are of about the same size, while the last is somewhat lower. The molar crowns, like those of the premolars, are implanted by two stout and subequal roots —a primitive condition opposed to the dryolestid root specialization.

Mandible.

The horizontal ramus is slender and its alveolar and lower borders are nearly straight and parallel in the region of the cheek teeth. The coronoid process arises a short distance behind the last molar at an angle of something over 45° to the alveolar border. Its apex is not preserved in any specimen, but apparently

it was slender and markedly recurved and separated from the condyle by a large, rather shallow notch. From the condyle there runs forward on the external face of the jaw a strong rounded ridge, which passes into the surface of the horizontal ramus at the anterior end of the masseteric fossa. It forms the inferior boundary of the fossa. This fossa is very well delimited, ending anteriorly in a small blind forward-projecting pocket: its antero-superior border of the fossa is formed by a ridge along the basal anterior part of the coronoid, which passes on to the horizontal ramus and curves forward, becoming obsolete under the anterior molar. The angle is no longer preserved on the type-specimen, where it was figured by Owen, but fortunately it is well seen on a specimen not hitherto described, 47799. It is a flattened triangular process, not continuing backward the curve of the lower border but abruptly jutting down from the latter. As Owen has stated, there is a suggestion of inflection, but not more so than in many placental mammals with angular processes which all agree to be non-inflected.

The pterygoid fossa is broadly excavated and is clearly demarcated inferiorly by a rounded ridge which originates from the anterior border of the angular process and which passes forward beneath the pterygoid fossa to its anterior end. The dental foramen in Mesozoic mammals generally is at the extreme anterior end of the pterygoid fossa, but in this form (as in the very remotely related *Spalacotherium*) the dental foramen is much farther back—here being at the inferior edge of the pterygoid fossa above the anterior end of the angular process. The internal groove begins just below the dental foramen and passes forward along the subpterygoid ridge to end rather abruptly a little behind a point below M_4. In two other specimens, 47751 and 47754, the groove may be traced forward somewhat farther, although it is not very definite anteriorly.

There are two widely separated main mental foramina, one beneath P_1 and the other beneath the posterior root of P_4, 47739, between P_4 and M_1, 47742, or beneath M_1, 47744. In the latter specimen there also appear to be two other smaller foramina in the incisive region.

MEASUREMENTS.

Lengths in millimetres:

	P_1.	P_2.	P_3.	P_4.	P_{1-4}.	M_1.	M_2.	M_3.	M_4.	M_{2-4}.
47739..	0·5	0·6	0·7	1·0	3·2	0·9	1·0	0·9	0·9	2·7
47742..	—	—	—	—	—	1·2	1·2	1·2	1·0	3·3
47744..	0·5	0·7	0·7	1·0	3·2	0·9	1·0	—	—	—
47751..	—	—	—	—	—	1·0	1·0	1·2	—	—
47754..	—	—	—	—	—	—	1·0	—	—	—
48404..	—	—	—	—	—	—	1·1	1·1	1·0	3·3

The species is a variable one as regards size, and it may eventually prove that there are really two distinct species, a larger one (47742 and 48404) and a smaller one (all the rest). Such a view, however, certainly is not supported by the evidence now in hand. The size variation is no greater than in many good species, and the morphology is the same so far as the material permits its determination.

Family DICROCYNODONTIDAE Marsh.

Diagnosis.—Pantotheria with upper and lower molars subquadrate, lower molars supported by two subequal roots and with large basined heels and two talonid cusps. Cheek teeth little reduced in number, jaw long and slender.

Discussion.—This peculiar and rather isolated family has hitherto been known only from America and seemed unlikely to occur in the collections from Europe. An unstudied specimen from the Purbeckian, however, the teeth of which had not been cleared from the matrix, has given unexpected and indubitable proof of the existence of the family in England in the Upper Jurassic. All but one of the known Upper Jurassic families of mammals are now seen to be common to the Purbeck and the Morrison.

Genus PERAIOCYNODON nov.

Diagnosis.—Dicrocynodontidae with five molars in the genoholotype (possibly one or two more in a fully adult individual). Lower molars with a basined heel with one external and one internal cusp. Trigonid subtriangular, narrower anteriorly than posteriorly, with three distinct coronal cusps, a very small cuspule anterior to the me^{d}, and a shelf-like antero-internal basal cusp.

The name is derived from περαῖος, dwelling beyond the sea, κύων, dog, ὀδούς, tooth, and is meant to recall its relative *Dicrocynodon* in sound.

Genotype.—*P. inexpectatus*, sp. nov.

This new genus casts welcome light on the problem of the origin of the group. The outstanding difference from *Dicrocynodon* in its molar pattern lies in the narrower more triangular trigonid, with the antero-internal cusp only slightly developed. These are primitive characters, and in these respects *Peraiocynodon* is certainly the less specialized genus of the two, although it is just as true a dicrocynodontid and has just as specialized a heel.

The *Peraiocynodon* molar compares in an interesting way with that of *Peramus*, which it resembles much more than does *Dicrocynodon*. If the *Peramus* trigonid were to become basined by the upgrowth of a curving ridge between the pa^{d} and me^{d} and if its talonid simultaneously broadened and became basined, it would essentially become *Peraiocynodon*. Continuance of the same sort of specialization would lead to *Dicrocynodon*. One interesting feature learned from this series is that it is apparently not the antero-internal cusp of *Dicrocynodon* which represents the pa^{d} as would naturally be supposed, but the antero-external one.

As has already been emphasized, the *Peramus* molar is a primitive one in general features. The dicrocynodonts branched off from the more normal pantotheres at a time long before *Peramus* itself appeared, so far as known, but there is good reason to believe that they were derived from a primitive pantothere much like this genus.

Peraiocynodon inexpectatus sp. nov.

(Pl. VIII, figs. 7–8 ; Text-figs. 35–36, 39.)

DIAGNOSIS.—(The only species of the genus.) Length of first four molars about 4·5 mm.

FORMATION AND LOCALITY.—Purbeckian of Durdlestone Bay, Swanage, Dorsetshire.

MATERIAL.—The following specimen is in the British Museum :

48248. Holotype. Part of left mandibular ramus with M_{1-4} and the germ of M_5. (*Beckles Colln. Purchased* 1876.)

DENTITION.

MOLARS.—The four teeth preserved form a graded series from the very small first one to the large and complicated fourth. It is apparent that they all belong to one set and hence are all molars. It is highly probable that the first tooth preserved is M_1. Behind M_4 is a clearly defined tooth germ, making five molars in all, although the individual is young and one or at most two more might be found in the adult.

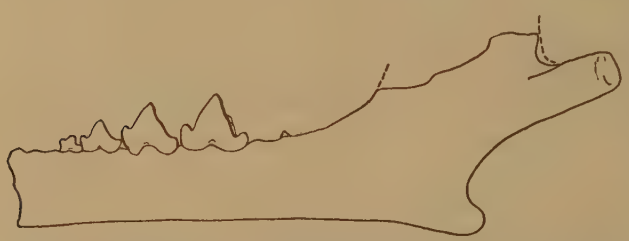


FIG. 39.—*Peraiocynodon inexpectatus* Simpson. External view of left mandibular ramus, holotype. × 6 diam. Upper Jurassic, middle Purbeck beds, Swanage, Dorset.

The most characteristic molar is M_4 and it may first be described. The crown is dominated by the stout, sharp pr^d, external in position and slightly anterior to the middle of the tooth. Its posterior contour, as seen from the outside, is concave and its anterior convex. Three vertical angulations or crests run from its apex : one anteriorly, one posteriorly, and one internally and somewhat posteriorly. The anterior one runs to a small cusp which is anterior and very slightly internal to the pr^d, apparently the homologue of the pa^d of *Peramus* and of the antero-external cusp of *Dicrocynodon* although the latter would not be identified as a pa^d without this intermediate step. Below and internal to this cusp is a small anterior heel, as in *Dicrocynodon* but less strongly developed. The pa^d sends a slight crest inward and a little backward which curves posteriorly along the internal border, becoming a slight cingulum-like shelf and passing back into the me^d. This shelf bears a faint suggestion of a cusp just anterior to the me^d, in the position occupied in *Dicrocynodon* by the more distinctly developed antero-internal cusp. While little over half as high as the much smaller pr^d, the me^d is the second cusp of the tooth in size. It is postero-internal to the pr^d, with which it is united by the sharp crest already noted, and has the appearance of being plastered on the inside of the pr^d, of being, indeed, merely an apex of an internal cingulum.

The heel is both long and broad and is basined and has not one but two cusps.

The external one is the larger, and is rather greater in size but lower in elevation than the supposed pa^d. It is directly posterior to the pr^d. The internal heel cusp, just posterior to the me^d, is more anterior in position than the external one and not so distinct. The resemblance to *Dicrocynodon* goes so far as to include the furrowing of the slopes of the pr^d, although the pattern of the furrows is not quite the same. Two of them pass down the antero-internal slope into the trigonid basin and two pass down the posterior slope into the talonid basin.

M_3 is much like M_4 save for being smaller and narrower. The furrows are less prominent, the smaller cusps less distinct. M_2 is still smaller and still narrower both absolutely and relatively, so that the anterior end now appears to be transversely compressed like that of a premolar. Even the me^d is not very distinct and there are no furrows on the pr^d, nor does the small anterior basal shelf appear to be developed. The talonid is still basined, however. M_1 is very minute and rather uncharacteristic. There is no distinct me^d on the internal cingulum, but the tiny talonid is still basined.

Mandible.

The lower jaw, seen only in external view, is also of a type closely approaching that of the American dicrocynodonts. The molar portion of the ramus is slender and straight with alveolar and lower borders nearly parallel. The posterior part of the jaw is remarkable in its almost complete lack of relief. There is no masseteric fossa or crest and the surface is nearly plane. The coronoid process arose in a gentle curve some distance behind M_5; further molars may, as already stated, have appeared later in life. The condyle faces more backwards than upwards, is strongly peduncular, and rises a slight distance above the molar level. The small angular process is placed rather far forward, more like that of *Peramus* than of *Amblotherium* or *Phascolestes*. It is rounded but slightly hook-like and its lower (anterior) border curves down somewhat from the lower border of the ramus, with which it is continuous.

It is interesting, but probably not important, that the peculiar striate nature of the bone which led Marsh to give the trivial name *striatus* to one of the American Dicrocynodonts is seen in this English form also.

Measurements.

	mm.
48248: Lengths—M_1	0·6
M_2	1·1
M_3	1·3
M_4	1·6
Depth of ramus outside below M_4	1·8
Distance from posterior end of M_4 to condyle	8·5

Family DRYOLESTIDAE Marsh.

Diagnosis.—Pantotheria with lower molars with four cusps, shortened anteroposteriorly. Talonid narrow, triangular in contour, with cusp internal in position. Me^d comparable to pr^d in height. Lower molar crown supported by a large root and

a smaller, wholly internal one. Cheek teeth little reduced in number. Jaw long and slender.

Discussion.—The various genera now placed in this family are so closely allied and so strikingly similar that it is very surprising to find that they have seldom been placed in a single family before. Marsh at first placed them in two families, Dryolestidae and Stylodontidae (1879), but he later united these two families under the former name (1887, p. 334). At this time he clearly stated that *Dryolestes* and its allies, American and English, and *Stylacodon* and its allies all have essentially the same type of molars—a truth which has since been entirely lost sight of.

Osborn at first (1888A) placed the dryolestids in the families Peralestidae, Kurtodontidae, Amblotheriidae, and Stylacodontidae, but in the same year he suppressed the families Peralestidae and Kurtodontidae (1888B). In 1907 Osborn united his so-called Amblotheriidae or Stylacodontidae into a single family; but Gregory (1922) has recently reverted to less correct views and places some in the Amphitheriidae and some in the Stylodontidae. This division rests on the very widespread error which supposes the molars of some of the dryolestids (so-called "stylodonts") to be much compressed, columnar, with connate roots. As a matter of fact, the number and proportions of the cusps are the same in these supposed stylodonts as in the typical dryolestids; the trigonid is, if anything, not shorter, as always stated, but *longer;* the talonid is similar in development and the roots the same. The reason for this error, almost universal except for Marsh's neglected correction of it in 1887, will become apparent when *Amblotherium* is studied.

The number of genera in the family is much reduced by the correction of this and of other errors. Of genera based on lower jaws there are now recognized only *Dryolestes*, *Laolestes*, *Kepolestes*, and *Amblotherium*, from the American Morrison, and *Amblotherium*, *Peraspalax*, and *Phascolestes* from the English Purbeck. These genera differ from one another only in relatively slight details, of which the evolutionary importance is not clear. All stand at about the same evolutionary level.

Genus AMBLOTHERIUM Owen.

(Text-figs. 35–36, 40.)

1866. *Stylodon* Owen, *Geol. Mag. London*, III, p. 199.
Non *Stylodon* Beck, 1837, *Ind. M.*, p. 46.
1871. *Amblotherium* Owen, "Fos. Mam. Mesozoic," p. 29.
1871. *Achyrodon* Owen, "Fos. Mam. Mesozoic," p. 37.
1879. *Stylacodon* Marsh, *Amer. Journ. Sci.*, (3), XVIII, p. 60.
1887. *Laodon* Marsh, *Amer. Journ. Sci.*, (3), XXXIII, p. 337.
1898. *Odontostylus* Trouessart, "Cat. Mam.," p. 1247.
Non *Odontostylus* Gray, 1840.
1899. *Trouessartia* Cossman, *Rév. crit. Paléont.*, April [May], 1899, p. 30
Non *Trouessartia* Canestrini and Kramer, Jan., 1899, *Bull. Soc. Études Sci.*, Angers, p. 59.
1899. *Trouessartiella* Cossman, in Trouessart's "Cat. Mamm.," new ed., fasc. VI, p. 1433, footnote.

Diagnosis.—Dryolestidae with dental formula I_4 C_1 P_4 M_{7-9}. Premolars slender, recurved, with no anterior cusp. Trigonid cusps all sharp and slender, the

pa^{d} erect or nearly so and approaching the me^{d} in height. Jaw small and slender apex of coronoid produced backward into a sharp point.

GENOTYPE.—*A. pusillum* Owen.

DISCUSSION.—Osborn (1888B) was the first to suspect that some or all of the genera here united under *Amblotherium* were synonymous, but, as he pointed out, the final decision as to this must rest on a thorough revision of all the specimens, American and European, a revision then impossible. This suggestion, however, has not won much consideration, and even Osborn in a later work (1907, p. 23) speaks of the molars in the family Amblotheriidae or Stylacodontidae becoming "progressively styloid and piercing, finally with single fang," a statement based on the acceptance of the supposed distinctive characters of "*Stylodon*"—characters which now prove to be non-existent.

The lower molar of *Amblotherium* has been supposed to have a high external cusp, two low internal cusps, and a heel, and to be implanted by two roots, that of

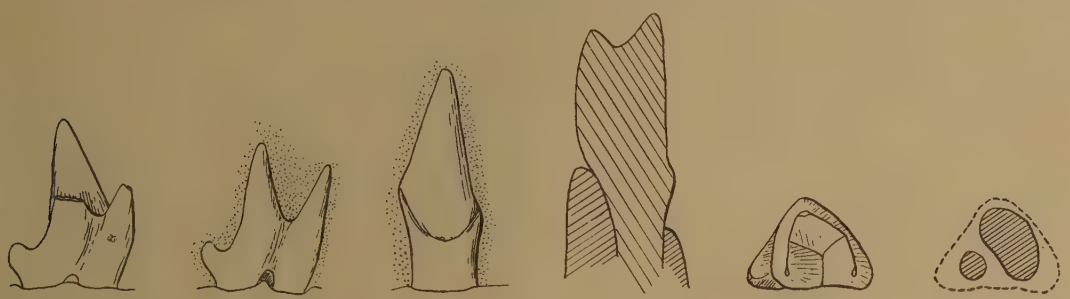


FIG. 40.—Diagrams of *Amblotherium* molar to explain former misapprehensions regarding its structure. A, internal view with paraconid and metaconid broken off as in Owen's conception of *Amblotherium*. B, internal view with cusps complete but protoconid buried in matrix, Owen's *Achyrodon*. C, external view with internal cusps buried in matrix, Owen's *Stylodon*. D, median, vertical, transverse section. E, crown view. F, horizontal section of roots. All × 20 diam.

Achyrodon was characterized by two slender cusps followed by a small heel and implanted by two roots, and that of *Stylodon* was believed to have but a single columnar cusp, taller than those of the other genera, without a heel and implanted by a single stout root. Re-study shows that all of these conceptions were due to the inadequacy of the material and its imperfect preparation (Fig. 40). *Amblotherium* is seen in internal view and has the me^{d} broken off. *Achyrodon* is the same thing with the me^{d} unbroken and the pr^{d} concealed by the matrix. *Stylodon* is the same genus in external aspect. It is taller because the alveolar mouth is lower externally. It has but one cusp because the others are buried in the matrix. It has no heel for the same reason. It has but one root because the peculiar arrangement of these in all members of this family makes only one root visible externally although two are seen internally. The appearance of *Amblotherium*, *Achyrodon*, and *Stylodon* is indeed very different, and it is not surprising that their true characters have been misunderstood, but they are all one and the same genus. For this genus the name *Amblotherium* is available; *Stylodon* was proposed first, but is preoccupied.

Turning to the American forms, one finds that here too the same genus has received two names: *Stylacodon* is the external aspect, and *Laodon* the internal aspect. Furthermore, this genus cannot at present be distinguished from the English *Amblotherium*, and the latter name thus is to be applied to it also.

Five of Owen's species are now referred to *Amblotherium*, but recognition of their true affinities enables one to reduce them to two—*A. pusillum*, the genotype, and *A. nanum*. There are also two American species, *A. gracilis* and *A. debilis*, to be fully described elsewhere. The differences between the various species are slight, and their adaptive or phylogenetic significance eludes us at present.

Amblotherium pusillum (Owen).

(Pl. IX., figs. 1–8; Text-figs. 41–42.)

1866. *Stylodon pusillus* Owen, *Geol. Mag. London*, III, p. 199.
1871. *Amblotherium soricinum* Owen, "Fos. Mam. Mesozoic," p. 29.
1871. *Achyrodon pusillus* Owen, "Fos. Mam. Mesozoic," p. 39.
1871. *Stylodon robustus* Owen, "Fos. Mam. Mesozoic," p. 52.
See also Lydekker, 1887, pp. 274, 277, 290; Osborn, 1888A, pp. 199, 207, and 1888B, p. 300.

DIAGNOSIS.—Me^d very slender and sharp, pa^d and me^d not very closely approximated. Pa^d nearly erect. Length of M_{1-6} about 5·0 mm. Horizontal ramus slender. Posterior rim of upper molars cuspidate.

FORMATION AND LOCALITY.—Purbeckian of Durdlestone Bay, Swanage, Dorset.

MATERIAL.—All the known specimens are in the British Museum, and all but the holotype are from the Beckles Colln. (*Purchased* 1876.)

M 5632. Part of left ramus, outer aspect, with P_4 and M_{1-7}. Holotype. Figd., Owen, 1866, pl. x, and 1871, pl. ii, fig. 15. (*Brodie Colln.*)

47743. Part of left ramus, external aspect, with I_{2-4}, C, P_1, P_3 and M_{1-2}. Figd., as *Peramus tenuirostris*, Owen, 1871, pl. ii, fig. 11.

47746. Part of left ramus, internal aspect, with P_2, P_4 and M_{1-5}. Figd., as *Achyrodon nanus*, Owen, 1871, pl. ii, fig. 6.

47747. Fragment of left ramus, internal aspect, with parts of two broken molars. Holotype of *Achyrodon pusillus*. Figd., Owen, 1871, pl. ii, fig. 8.

47752. Right ramus, internal aspect, nearly complete, with I_{1-4}, C, P_{1-4} and M_{1-6}. Holotype of *Amblotherium soricinum*. Figd., Owen, 1871, pl. ii, fig. 1; Osborn, 1888A, pl. ix, fig. 11.

47756. Right lower jaw with five molars, associated left lower jaw with fragments of premolars and molars and associated right upper jaw with four molars. Reference to this species is probable but not certain. Figd., as *Stylodon pusillus*, Owen, 1871, pl. ii, fig. 16.

47757. Left mandibular ramus with I_{1-2}, C, P_{3-4} and M_{1-7}. Figd., as *Stylodon pusillus*, Owen, 1871, pl. ii, fig. 17; as *Stylacodon pusillus*, Osborn, 1888A, pl. ix, fig. 14.

47759. Left ramus, external aspect, with M_{6-7} and roots or bases of P_4 and M_{1-5}. Figd., as *Stylodon pusillus*, Owen, 1871, pl. ii, fig. 19.

47761. Left ramus, external aspect. P_4 and M_{1-6}. Figd., as *Stylodon pusillus*, Owen, 1871, pl. iii, fig. 3.

47762. Left ramus, external aspect. P_4, M_1 and M_{3-8}. Holotype of *Stylodon robustus*. Figd., Owen, 1871, pl. iii, fig. 1.

47783. Left ramus, internal aspect, with four molars. Figd., as *Achyrodon nanus*, Owen, 1871, pl. ii, fig. 7.

47787. Part of left maxilla with two premolars and fragments of three molars. Reference to this species is probable but not certain.

47802. Part of right maxilla with a premolar and three broken molars.

M 10927. Part of left ramus with C, and M_{1-7}, internal aspect.

Dental Formula.

The specimen 47752 clearly shows the presence of four incisors, a canine, and four premolars. In this specimen there are six molars and alveoli for one more, making seven. The teeth are relatively little worn, and it is possible that another molar may have been erupted later in life. M 10927, a specimen which shows the molars very well but which has not previously been studied, was of about the same age as the type. M_7 is not fully erupted. Behind it the jaw has been cut away and there appears to be a germ for M_8, but this is not certain. In 47745 there are eight molars in place, and this is also true of 47762 and M 5632 (in the last M_8 is missing, but its alveolus is unmistakable). It thus appears that the species had eight molars, of which the last was rather tardy in appearing. In 47746, however, there are five molars, which are very badly worn and indicate a senile individual, and these are followed by the unmistakable alveoli for four more, making nine in all. Either nine was definitive for the species, with the last coming into use only in the aged, or else this is an individual anomaly. As nine is a higher number of molars than occurs in any other known Mesozoic mammal, or indeed in any mammal whatsoever, save possibly for some edentates or cetaceans, the latter alternative seems the more probable. The dental formula $I_4 . C_1 . P_4 . M_{7-9}$. thus conforms with all the observed facts, and $I_4 . C_1 . P_4 . M_8$ may be considered typical of the species (and of the genus of which it is the type).

Lower Dentition.

Incisors.—The four incisors are seen in internal view in the type, and the first two in external view in 47757. They are serial in arrangement, the first being but little more internal than the last. I_1 is procumbent, continuing forward the curve of the lower border. Its crown is hollowed out supero-posteriorly so as to be spatulate—an appearance accentuated in I_{2-3} which are progressively shorter and less procumbent. I_4 is nearly erect. As seen it is near the canine and there is a gap in front of it, but it is apparently broken, and these would not be its relationships in life. Originally the incisors were evenly spaced and their rounded tips rose to about the same level, the anterior, more procumbent, ones being longer.

Canine.—The canine is of moderate size, taller than any other tooth in the

jaw, simply pointed, the tip somewhat recurved, the postero-internal surface somewhat excavated. In the type it appears to be erect, but this may be due to crushing; in the other specimens in which it is preserved it is somewhat procumbent. In some cases there is a faint indication of a median longitudinal groove near the alveolus, but this is not very definite. It was probably one-fanged, but if there were two roots they were little divergent and incompletely separate.

PREMOLARS.—The premolars are identical in pattern but increase in size from first to fourth. Each consists of a piercing central cone, somewhat compressed transversely, the anterior profile convex, the posterior one equally concave. There is no accessory cusp above the heel, which is small and rises to form a true cingulum cusp. The internal cingulum is very feeble and rounded, and becomes obsolete before reaching the anterior end of the tooth. The external face is smoothly convex, without a cingulum. Each of the premolars is implanted by two roots of about equal size.

MOLARS.—The molars are so fragile and their graceful cusps so liable to damage that in specimens showing the more important view, the internal one, they are usually badly broken. In the type only two cusps of its six preserved molars are unbroken. The most instructive specimen is the hitherto undescribed M 10927, although even it is somewhat broken. The pr^d is remarkably slender and sharp. Its antero-internal face, passing down into the trigonid basin, is distinctly concave. The me^d is also slender and sharp and is directly internal to the pr^d, with which it is united by a sharp transverse crest. It is quite vertical. The pa^d, like the other trigonid cusps, is slender and sharp, and is nearly erect, pointing but little forward It is nearly as high as the me^d. The internal bases of the pa^d and me^d are convex and are separated by a nearly vertical groove.

The low and narrow heel is somewhat globose internally. It is slightly internal on each tooth to the succeeding pa^d, so that the molars seem to overlap slightly. The talonid shelf narrows and falls as it passes externally and it is continuous with the rounded cingulum which passes round the external part of the base of the pr^d and then up on to the antero-external face, where it becomes obsolete. Except for this cingulum the external aspect of the pr^d is smoothly convex and, as has been so often emphasized for "*Stylodon*," it is lofty, styloid, and piercing.

Each molar is implanted by two roots, a large one, occupying the whole of the external part of the base and the antero-internal part, and a small one confined to the postero-internal corner of the tooth.

The molars increase in height to M_{4-5} and then decrease slightly again to M_8. The anterior molars are somewhat longer relative to their width than the posterior ones. M_1 is rather atypical, the disparity in height between talonid and trigonid being less and the pa^d pointing more forward.

LOWER JAW.

The horizontal ramus is long and slender, especially as seen from the outside. The alveolar border is straight internally, less so externally because of the lowering

of the alveolar lips under the middle molars. The lower border forms a gentle convex curve at its lowest beneath M_5. The anterior border of the coronoid rises at a steep angle immediately behind the last molar (whether this be the seventh or ninth) and then curves back to a sharp, slender, posteriorly directed point, exactly as in *Amblotherium* (*Stylacodon*) *gracilis* (Marsh). (Marsh, 1887, pl. ix, fig. 1.) Indeed, all the mandibular features are closely similar to those of the cited American specimen and strongly support the evidence of the dentition that this species is congeneric with *Amblotherium soricinum*. The supracondylar notch is deep and almost circular, nearly 270° of a circle being represented when the coronoid was complete. The condylar process does not have a constricted neck, and it rises far above the molar level. The articular surface is missing. As in dryolestids generally, the angle is small and styloid and continues the contour of the lower border backward with slight change in curvature. When complete, the angle extended back to a point directly beneath the posterior end of the condylar process. Along the inner surface of the angle runs the well-defined pterygoid crest, passing forward to a point just below the dental foramen, at the antero-inferior corner of the shallow and poorly marked

FIG. 41.—*Amblotherium pusillum* (Owen). External view of some of right upper cheek teeth. B.M. 47882. × 12 diam. Upper Jurassic, middle Purbeck beds, Swanage, Somersetshire.

pterygoid fossa. From a point immediately in advance of the dental foramen, the linear internal groove curves forward and downward, to pass upward again slightly and end at the posterior end of the long symphysial surface, beneath P_3.

The masseteric fossa is rather deep but its boundaries are rounded. It is pointed anteriorly and passes into a median longitudinal groove on the horizontal ramus which soon becomes obsolete anteriorly. In 47757 there is one large mental foramen, beneath the posterior end of P_2. In 47761 there is also a smaller one beneath P_3.

UPPER DENTITION.

Amblotherium pusillum is one of the three species of Jurassic mammals in which the upper and lower molars are found in actual possession. Owen noticed this fact, but he did not give any description of the upper molars of the specimen concerned (47756), which he referred to *Stylodon pusillus*. Both Osborn and Lydekker seem to have overlooked the presence of upper molars in this specimen. Fortunately, the fragment has been crushed in such a way as to bring the crowns of the upper molars fully into view despite the fact that they are still interlocked with the lowers, and their characters can be fairly well made out. Comparison with other specimens seems to warrant reference of 47787 and 47802 to the same species.

PREMOLARS.—There were apparently four upper premolars, the second being seen in 47802 and the third and fourth in 47787. They are all alike save for a slight regular increase in size. Even P^4, however, is smaller and lower than the

succeeding molars, in contrast to the condition in the lower jaw. Each has a slightly compressed central cusp of moderate height, with a small anterior accessory cusp and a lower but larger posterior heel. There is a faint suggestion of an internal cingulum on P^4, but otherwise they are without cingula internal or external. They are less lofty, slender, and recurved than the lower premolars.

Molars.—The number of upper molars cannot be made out but it was probably either seven or eight, as the number of upper molars in this group is generally one less than of lower molars.

M^2 is about as broad (transversely) as long (longitudinally) ; the more posterior teeth are broader than long. The crown is obliquely triangular. The outer border follows the external border of the alveolar process of the maxilla ; the anterior border is at right angles to this ; and the posterior border is oblique. The molars preserved are thus essentially right triangles, the hypotenuse postero-internal and the shorter side external after M^2. The crown is a shallow basin with sharp raised edges, the external edge being the lowest. The anterior rim culminates externally in a small marginal cusp, while the posterior rim bears two small cusps, neither of which is truly external. The postero-external angle of the crown is not truly cusped but is slightly elevated and lip-like. Antero-external to the basin is a small hook-like projection or heel. The whole crown is dominated by the internal apex which rises into a sub-crescentic cusp higher than any other on the tooth. The anterior and posterior raised rims of the basin pass up to the apex of this cusp, giving it its crescentic aspect. The apex of this cusp is not quite erect, but points a little posteriorly. There is no median transverse ridge.

Fig. 42.—*Amblotherium pusillum* (Owen). Crown view of upper molars and external view of associated lower molars. B.M. 47756. × 12 diam. Upper Jurassic, middle Purbeck beds, Swanage, Dorsetshire.

None of these specimens preserves enough of the maxilla to yield any information of value.

Measurements.

Maximum lengths in millimetres :

	C.	P_1.	P_2.	P_3.	P_4.	M_1.	M_2.	M_3.	M_4.	M_5.	M_6.	M_7.	M_{1-6}.
47752	0·5	0·4	0·5	0·7	0·8	0·8	0·8	0·9	0·9	0·9	0·9	—	4·9
47746	—	—	—	—	—	—	—	—	—	—	—	—	*ca.*4·9
47757	—	—	—	—	—	—	—	—	—	—	—	—	5·0
47759	—	—	—	—	—	—	—	—	—	—	0·9	0·8	—
47761	—	—	—	—	—	—	—	—	—	—	—	—	5·1
47762	—	—	—	—	—	—	—	—	—	—	—	—	5·1
M 5632	—	—	—	—	—	—	—	—	—	—	—	—	5·2
M 10927	—	—	0·6	—	—	0·8	0·9	0·9	0·9	0·9	0·9	0·7	5·0

Total length between verticals :

47752 .. .. .. Ca 18·5 mm.

Depth below M_3 inside:

47752	2·2
47746	2·1
47783	2·2
M 10927	2·1

Height, top of coronoid to bottom of angle:

47752	6·3

Amblotherium nanum (Owen).

(Pl. X, figs. 1–6; Text-figs. 43–44.)

1871. *Achyrodon nanus*, Owen, "Fos. Mam. Mesozoic," p. 37.
See also Lydekker, 1887, p. 276; Osborn 1888A, p. 201.

DIAGNOSIS.—Pa^d somewhat less erect and more closely approximated to the me^d, which is a little less slender and sharp. Length of M_{1-6} about 4·5 mm. Horizontal ramus somewhat deeper. Posterior rim of upper molars not cuspidate.

FORMATION AND LOCALITY.—Purbeckian of Durdlestone Bay, Swanage, Dorset.

MATERIAL.—All the known specimens are in the British Museum, Beckles Colln. (*Purchased* 1876.)

47745. Right ramus, internal aspect, with P_{3-4} and M_{1-8}. Holotype. Figured as *Achyrodon nanus*. Owen, 1871, pl. ii, fig. 5; Osborn, 1888A, pl. ix. fig. 13.

47758. Right and left mandibular rami, both in external aspect, with most of the teeth present, although somewhat broken. Most of a badly crushed associated skull with four right upper molars visible. A number of vertebrae and fragments of ribs. Lower jaw figd., as *Stylodon pusillus*, Owen, 1871, pl. ii, fig. 18.

47760. Left ramus, external aspect, with P_4 and M_{1-7}. Figd., as *Stylodon pusillus*, Owen, 1871, pl. iii, fig. 2.

47785. Left ramus, internal aspect, with M_{2-5} and M_8.

47786. Fragment of right ramus, internal aspect, with two broken molars. On the same slab, but not in definite association, is a right maxilla with the last two premolars and all seven of the molars. The reference of these two fragments to the same individual, and reference of the individual to this species, is not certain but is probable.

48403. Right maxilla with M_{1-6}. Reference to this species is probable.

LOWER DENTITION.

PREMOLARS.—The premolars are exactly like those of *A. soricinum*, so far as observed.

MOLARS.—The molars are built on the same plan as those of *A. pusillum*, but they appear to differ in a number of minor details. The me^d is more columnar,

less slender, less pointed, the pa^d shorter and less erect. Both these differences might be accentuated by wear, but comparison of various specimens seems to indicate that they are not wholly due to this cause. These two cusps are also more closely approximated, and the notch between them is a mere V-shaped slit, instead of being more nearly U-shaped as in the genotype. The talonid, at least in some specimens and perhaps in all, is confined to the internal part of the crown, instead of extending externally as a shelf as it does in most pantotheres, and the external cingulum is very weak or absent. The length of the molar series is also somewhat less than in the genotype.

These differences, with others equally marked in the upper molars, leave no doubt as to the validity of this species. If a large series of well-preserved material were available, it is even possible that it would be found convenient to separate *A. pusillum* and *A. nanum* generically, but this certainly cannot be done to advantage on the basis of the specimens now in hand.

Owen based his genus *Achyrodon* chiefly on the supposed features that in this form the me^d was sharp and slender, the pa^d similar and nearly as high, the eight molars occupying the same space as the seven of *Amblotherium soricinum*. The first two features are true of *Amblotherium* to an even more marked degree than they are of "*Achyrodon*"; the last is certainly not a character on which a generic distinction could be based.

Mandible.

The horizontal ramus is distinctly stouter relative to the teeth than it is in the genotype. The anterior border of the coronoid appears to arise more steeply, but the difference is slight and perhaps illusory. The division of the anterior end of the pterygoid fossa into two depressions, noted by Osborn, does not actually occur. Pterygoid crest, dental foramen, internal groove, and other observable mandibular features are almost exactly as in *A. pusillum*.

Upper Dentition.

In this species, also, upper and lower molars have been found in actual association. In 47758 the association is obvious, while in 47786 upper and lower jaws are about an inch apart and the association is merely presumptive. 48403, including only upper teeth, is also to be referred to this species with some probability.

Premolars.—Only the last two premolars are known. The penultimate, probably P^3, is small and agrees with the corresponding tooth of *A. pusillum*. P^4 is much larger, with a high pointed main cusp, nearly conical but slightly compressed transversely, and somewhat recurved. From its apex runs postero-externally a sharp crest just anterior to which is a vertical concavity terminating, near the base of the tooth, in the basin of a small postero-external heel. There is no anterior crest from the apex of the tooth, but there is a small antero-external heel at a level somewhat farther from the alveolus than the posterior one. There is no true external cingulum and no internal cingulum.

Molars.—The entire molar series is known. It consists of seven teeth of much

the same structure but varying greatly in shape and proportions. Thus M^1 is about as long as broad and M^5 is much produced transversely and shortened longitudinally. The interspaces between the teeth are very narrow, probably even narrower than in life. The crown is built on the same plan as in *A. pusillum*, but there are very distinct differences at least of specific and possibly of generic value. The posterior border is a simple, sharp raised rim, without the two small cusps developed here in the genotype. The external cusp terminating the anterior crest is small and just posterior to it there is developed a very slight median external elevation of the border. The latter may possibly have been present also in the genotype, for it would soon be obliterated by wear. The heel at the antero-external angle projects more anteriorly on M^{1-2}, but more and more externally on the more posterior teeth. On M^5 there is a rudiment of a transverse median crest in the basin, running from the internal cusp to the minute centro-external one, and a faint suggestion of such a rounded ridge is also seen on M^4. Indeed, in 48403 there is reason to believe that this feature was present on all the molars, but it is very slight. The external border of the crown is notched slightly in the centre, as seen from below.

The internal cusps are nearly in a straight line, so that the outer borders form a convex curve in accordance with the varying widths of the teeth. This width

FIG. 43.—*Amblotherium nanum* (Owen). Last premolar and upper molars of B.M. 47786. A, external view. B, crown view. × 6 diam. Upper Jurassic, middle Purbeck beds, Swanage, Dorsetshire.

increases slightly from M^1 to M^5 and then M^{6-7} are more abruptly narrower. M^7 is small and does not show the distinct development of outer cusps seen in the other molars, nor has it the median notch in the external contour.

SKULL.

In number 47758 most of the skull is preserved, but unfortunately it is so badly crushed that it has not been possible to make a reconstruction, and none of the basicranial features can be certainly determined. The cranial roof is shown, rather obscurely. The cerebellar and cerebral fossae have about the same relationships and relative sizes as in *Triconodon*, although it seems probable that the hemispheres were somewhat more expanded. The olfactory bulbs seem to have been smaller than in *Triconodon*, although the nature of the material does not permit positive determination of this feature. The skull had a small, elongated, rounded brain case preceded by a long narrow snout.

SKELETON.

There are associated with the above specimen a number of articulated or closely associated vertebrae and some rib fragments. Like the skull, this material is poorly preserved, but its general features can be made out. The anterior of the preserved

vertebrae seem to be dorsals. The centrum is depressed, and the neural arch is low. The neural spine is represented only by a low longitudinal ridge on the flat upper surface of the neural arch. The zygapophyses are simple but relatively stout. There are no distinctly developed transverse processes, but on the posterior half of the lateral aspect of the centrum are two small longitudinal ridges enclosing a deep narrow groove between them. The ventral surfaces of the centra appear to be smoothly rounded. The preservation is not sufficiently good to determine the

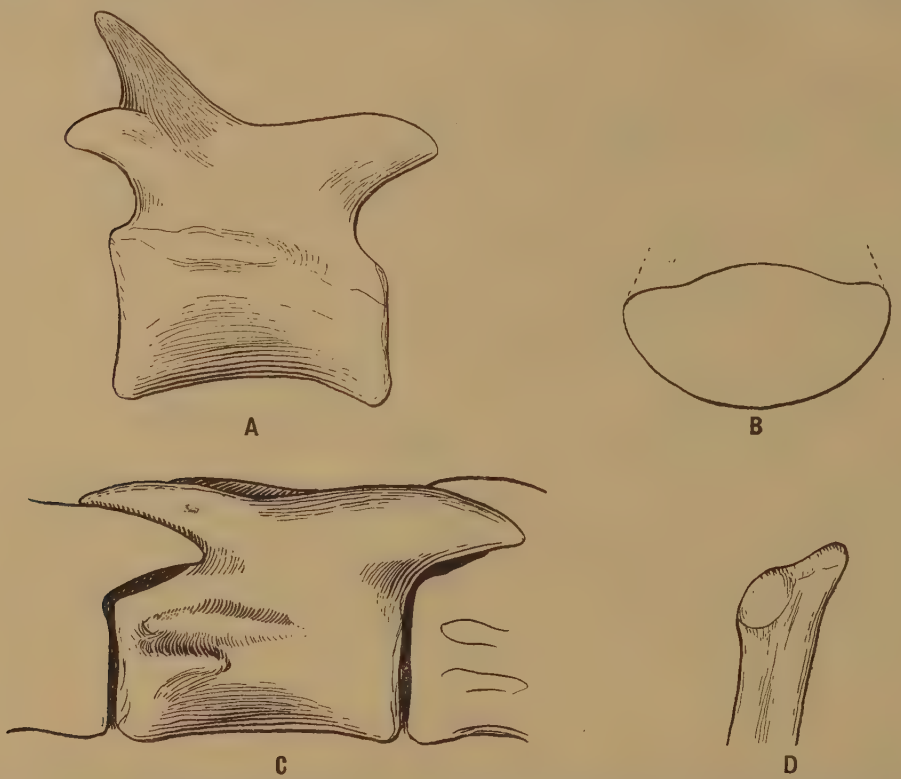


FIG. 44.—*Amblotherium nanum* (Owen). Skeletal parts of B.M. 47758. A, lumbar vertebra, right lateral view. B, end view of centrum of lumbar vertebra. C, dorsal vertebra, right lateral view. D, head of rib. All × 15 diam.

articular facets for the ribs. Presumably the main or only facet was inter-vertebral and ventro-lateral.

The more posterior of the preserved vertebrae appear to be lumbars. They are similar to the dorsals, with the same depressed centra, and here, at least, the ends of the centra are both slightly concave. The neural arch appears to be higher than in the dorsal region, the intervertebral notches larger and more open. The neural spine is here a small, high, pointed, postero-superiorly directed process on the posterior part of the neural arch. The transverse process is either absent or is represented by a slight ridge at the junction of the centrum and arch posteriorly, although this apparent ridge may be due to crushing.

The ribs appear to be simple, one headed, somewhat flattened. In at least one case, however, there seems to be a tendency for the elongation and division of the articular face.

MEASUREMENTS.

		mm.
47745.	Length M_{1-8}	5·9
	Depth inside below M_7	2·7
48403.	Length M^{1-6}	4·8
	Width M^5	1·2
47786.	Length M^{1-6}	4·7
	Width M^5	1·3

Amblotherium sp. indet.

Under this heading are included the following two specimens from the Purbeckian of Durdlestone Bay, which are apparently amblotheres but are not specifically determinate. Both are from the Beckles Collection in the British Museum.

47800. Part of the right ramus, external aspect, with the teeth broken off at the roots, and an apparently naturally associated fragment of right upper jaw with four molars, badly worn and broken. These upper molars appear to agree most closely with *Amblotherium nanum*, but their preservation is inadequate for exact determination.

48389. Right ramus, internal aspect, with P_4 and M_{1-6} in poor preservation.

GENUS KURTODON Osborn.

1887. *Athrodon* Osborn, *Proc. Acad. Nat. Sci.*, Philadelphia, 1887, p. 290.
Non *Athrodon* Sauvage, 1880, *Bull. Soc. géol. France*, VIII, p. 530.

1887. *Kurtodon* Osborn, *Amer. Nat.*, 1887, p. 1020.

1892. *Curtodon* Zittel, " Handb. Palaeont.," IV, p. 102.

1893. *Cyrtodon* Winge, *E Museo Lundii*, 1893, p. 118.

DIAGNOSIS.—A genus of doubtful status, founded on a single dryolestid upper jaw. Dental formula $I^1\ C^1\ P^4\ M^7$. Molars with very feeble cusps, save the internal one, and with a distinct, rounded, transverse median ridge on each crown.

GENOTYPE.—*K. pusillus* Osborn.

DISCUSSION.—The specimen on which this genus is based was referred to *Stylodon* by Owen. Osborn placed it in a new genus, *Athrodon*, later changed to *Kurtodon*, stating that " the mandibular series of *S*[*tylodon*] *pusillus* . . . present many points of difference : there is no diastema, the premolars are erect and functional ; the molars are set in a straight line, they are slender and widely separate from each other . . . : the series are not subequal but diminish in both directions from the middle molar. . . . In *Kurtodon* there are, strictly speaking, no cusps, and the action of the jaws must have been chiefly horizontal. . . . It is clear that the two forms belong not only to distinct genera but to distinct families." (Osborn, 1888A, p. 210.) Lydekker had previously pointed out the apparent association of a stylodont lower jaw with an upper in 47786 (1887, p. 291), and this, together with a re-study of

the specimen itself, finally led Osborn to regard *Kurtodon* as a member of the group here united under the dryolestids (1888B, p. 300). He still writes, however, "The *Kurtodon* crowns are unlike those of *Amblotherium soricinum* or of *Achyrodon* since the summit is much broader and the wearing surface, instead of being trenchant, is grinding, as previously described . . ."

In fact, the diastema of *Kurtodon* is very small; the molars are cuspidate, they are trenchant along their anterior and posterior borders, they are not grinding, the interspaces are reduced by crushing and were originally quite large enough to accommodate the trigonid of any dryolestid of suitable gross size. The molars of *Amblotherium nanum* hardly seem, in themselves, generically distinct from those of *Kurtodon pusillus;* indeed, these two forms are about as closely similar as are *A. nanum* and *A. pusillum*. There are definite differences, however, and *Kurtodon* clearly did not belong to any known species of *Amblotherium*. Since it cannot be proven to be synonymous with any genus based on lower jaws, the genus *Kurtodon* is retained for the present, with the understanding that it is little different from *Amblotherium*. It may possibly represent the upper dentition of *Peraspalax* or *Phascolestes*.

Kurtodon pusillus Osborn.

(Pl. XI, figs. 1–2; Text-fig. 45.)

1887. *Athrodon pusillus* Osborn, *Proc. Acad. Nat. Sci.*, Philadelphia, 1887, p. 290.

1888. *Kurtodon pusillus* Osborn, *J. Acad. Nat. Sci.*, Philadelphia, IX, p. 208.

DIAGNOSIS.—(The only species of the genus.) Length M^{1-4} about 4 mm.

FORMATION AND LOCALITY.—Purbeckian of Durdlestone Bay, Swanage, Dorset.

MATERIAL.—The following specimens are in the British Museum, Beckles Colln. (*Purchased* 1876.)

47755. Much of left maxilla with *C*, P^{3-4}, and M^{1-7}. Holotype figd., as *Stylodon pusillus*, Owen, 1871, pl. ii, fig. 14; as *Kurtodon pusillus*, Osborn, 1888A, fig. 4 and pl. ix, fig. 15; 1888B, fig. 2*a*.

48402. Part of right maxilla with P^4 and M^{1-5}.

DENTITION.

CANINE.—The canine is a high, slender, recurved, conical tooth. The apex is now broken off, but was apparently sharply pointed. In cross section it is broadly elliptical, save for the presence of a slight keel posteriorly. There are two stout roots, which are very slightly divergent.

PREMOLARS.—The supposed columnar first premolar (Osborn) is now broken, what remains being only part of the single root. There follows a short diastema, not longer than the alveolus for P^1, and then the roots, apparently two in number, for the small P^2, P^3 and P^4 are preserved and are very like those of *Amblotherium nanum*.

MOLARS.—The molars, so far as preserved, are seven in number and are placed

much as in other dryolestids. The almost closed interdental embrasures and the concavity of the line of the internal cusps—conditions which led to a belief that the teeth overlapped those of the lower jaw instead of interlocking with them—are due to crushing. The variations in form between the different teeth are much as in the species already described.

As before, the molar crown is dominated by the high crescentic inner cusp. The wings of this crescent are low but sharp ridges, the anterior one passing externally along the anterior border of the tooth, the posterior one postero-externally along the posterior border. They enclose a smooth, slightly basined area. As the anterior crest curves round to pass into the equally elevated external rim of the basin it rises to form a small elongated marginal cusp. There is also a tendency to form a median external cuspule of very minute size, but on most of the teeth this is hardly to be distinguished from the rather larger cusp just described. The postero-external angle is somewhat produced and spout-like, but not truly cuspidate. There is also, as in all known dryolestid upper molars, an antero-external hook-like heel or parastyle, jutting anteriorly on the first few molars, antero-externally on the more posterior ones. Beginning at the apex of each internal cusp and running down its otherwise concave outer slope is a distinct, broadly rounded transverse ridge which passes down into the basin and becomes obsolete just before reaching the external rim.

FIG. 45.—*Kurtodon pusillus* Osborn. Crown view of left upper cheek teeth, holotype. × 5 diam. Upper Jurassic, middle Purbeck beds, Swanage, Dorsetshire.

M^5 and M^6 are more nearly alike than in *Amblotherium nanum* and M^7 is much less reduced relative to the other molars and less modified in form. It is possible that there was another molar, although there is no definite evidence of this and no more than seven are certainly known in the upper jaw of any pantothere.

MEASUREMENTS.

Maximum length in millimetres :

	C.	P_3.	P_4.	M_1.	M_2.	M_3.	M_4.	M_5.	M_6.	M_7.	M_{1-4}.
47755	1·4	0·9	1·2	0·9	1·0	1·1	1·3	1·1	1·0	0·9	4·1
48402	—	—	1·2	0·8	1·0	1·2	1·2	1·2	—	—	—

Width M_4 .. .. 1·5 mm.

GENUS PERASPALAX Owen, 1871.

1871. *Peraspalax* Owen, "Foss. Mamm. Mesozoic," p. 40.

DIAGNOSIS.—Dryolestidae with P_4 with a well-developed and cuspidate heel and with a distinct anterior cingulum cusp. Pa^d short, rounded, tapering, and pointing well forward. Trigonid basin large, less compressed antero-posteriorly than in *Phascolestes*.

GENOTYPE.—*P. talpoides* Owen.

DISCUSSION.—This genus is very close to *Phascolestes* and more material may prove these two to be identical, although the evidence in hand does not permit this conclusion. It is rather less like *Amblotherium* than is *Phascolestes*.

Peraspalax talpoides Owen.

1871. *Peraspalax talpoides*, Owen, "Fos. Mam. Mesozoic," p. 40.

1887. *Amblotheriuin talpoides*, Lydekker, "Cat. Fos. Mam. B.M. (N.H.)," p. 275.

DIAGNOSIS.—(The only species of the genus.) Length M^{2-7} about 6·3 mm.

FORMATION AND LOCALITY.—Purbeckian of Durdlestone Bay, Swanage, Dorset.

MATERIAL.—The following specimen is in the British Museum:

47738. Part of left ramus, internal aspect, with P_4 and M_{2-7}. Holotype, figd., Owen, 1871, pl. ii, fig. 9; Osborn, 1888A, pl. viii, fig. 9. (*Beckles Collection. Purchased* 1876.)

DENTITION.

PREMOLARS.—Only P_4 is preserved. The main cusp is succeeded by a heel which rises to a definite cusp and is better developed than in *Phascolestes*. The internal cingulum is not strong but is continuous and forms a small but definite cusp anteriorly.

MOLARS.—The molars are somewhat worn, but not enough to obscure their true characters, or to hide the distinctions from *Phascolestes*, especially when compared with equally worn molars of the latter. The general pattern is that of all dryolestids and is very close to *Phascolestes* in particular, but differs in having the trigonid less compressed antero-posteriorly, the pa^d more slender and tapering and pointing more forward, and the trigonid basin more open and rounded. This last may be due especially to wear, although wear does not have this effect on *Phascolestes*.

M_1 is missing, and there are alveoli for M_8, the total number being apparently eight as usual in dryolestids.

MEASUREMENTS.

Maximum lengths in millimetres:

P_4.	M_2.	M_3.	M_4.	M_5.	M_6.	M_7.	M_{2-7}.
1·1	0·9	1·0	1·2	1·3	1·4	1·3	6·3

Depth of ramus inside below M_5 .. .. 2·8

GENUS PHASCOLESTES Owen, 1871.

(Text-figs. 35–36.)

1871. *Phascolestes* Owen, "Foss. Mamm. Mesozoic," p. 35.

DIAGNOSIS.—Dryolestidae with P_4 blunt, erect, heel not distinctly cuspidate, no anterior cingulum cusp. Trigonid very short, compressed antero-posteriorly. Pr^d broad and blunt, as are also the me^d and pa^d. Me^d columnar. Pa^d shorter than me^d, nearly erect, subspatulate in internal aspect.

GENOTYPE.—*P. mustelula*, Owen.

DISCUSSION.—The molars of this genus have a very distinctive aspect, somewhat difficult to describe but very easy to recognize, which at once differentiates them

from all other pantotheres. It results from the shortness of the trigonid, the broad blunt cusps, and the peculiar, somewhat recurved or spatulate pa^4. The difference from *Amblotherium* is not profound, but is sufficient to prevent our following Lydekker and others in considering them synonymous.

Owen (1871, p. 35) proposed the name *Phascolestes* tentatively for a lower jaw which he referred to *Peralestes*, in case it should prove distinct. To this species ("*Peralestes* [*Phascolestes ?*] *longirostris*") Owen added a second one which he called simply "*Peralestes*, sp. ?" in his text, but called *Phascolestes dubius* in the legend to his plate. Osborn (1888A, pl. ix, fig. 12) erroneously applied the name *P. dubius* to Owen's *P. longirostris*. The two are certainly not conspecific. The proper type of *P. dubius* cannot be found. Owen's figure and description of it are entirely uncharacteristic and his referred specimen (1871, pl. i, fig. 41) is indeterminate, so that this species must be considered a *nomen nudum*.

Lydekker (1887, p. 275) indicated the synonymy of *P. longirostris* with the prior *Amblotherium mustelula*. In this he seems to have been quite correct, but *A. mustelula* is generically distinct from the genotype *Amblotherium soricinum*, so that the species must be called *Phascolestes mustelula*. It is the only known species of this genus.

Phascolestes mustelula (Owen).

(Pl. XI, figs. 4–6.)

1871. *Amblotherium mustelula* Owen, "Fos. Mam. Mesozoic," p. 31.

1871. *Peralestes* (*Phascolestes ?*) *longirostris* Owen, "Fos. Mam. Mesozoic," p. 35.

1888. *Phascolestes dubius* Osborn, *J. Acad. Nat. Sci.*, Philadelphia, IX, p. 200.

DIAGNOSIS.—(The only species of the genus.) Length M_{1-5} about 5·0 mm.

FORMATION AND LOCALITY.—Purbeckian of Durdlestone Bay, Swanage, Dorset.

MATERIAL.—All known specimens are in the British Museum, Beckles Colln. (*Purchased* 1876.)

47753. Right mandibular ramus, nearly complete, internal aspect with base of canine, stumps of premolars, M_{1-5} and M_7. Holotype figd., as *Amblotherium mustelula*, Owen, 1871, pl. ii, fig. 2.

47741. Part of left ramus, internal aspect, with I_{1-4}, C, base of P_1, P_{2-4}, and M_{1-5}, somewhat broken. Holotype of *Phascolestes longirostris* Owen. Figd., Owen, 1871, pl. ii, fig. 4; Osborn, 1888A, pl. ix, fig. 12, as *Phascolestes dubius*.

47808. Crushed right ramus, lacking the coronoid process, internal aspect, with I_{3-4}, C, P_4, M_{1-5} and M_{7-8}.

LOWER DENTITION.

INCISORS.—The four somewhat procumbent incisors are of the subspatulate type common, so far as known, to all pantotheres. I_1 is antero-internal to I_2 and

I_{2-4} are in an antero-posterior series. The teeth are closely crowded and there is no precanine diastema.

CANINE.—The canine is erect and is unusually tall and slender, the apex somewhat recurved as usual. It has two roots.

PREMOLARS.—P_{1-2} are very small relative to P_{3-4}. The latter are of about the same length, but P_4 is noticeably higher. They are much like those of *Amblotherium*, but less sharp and recurved. The internal cingulum is very faint and rounded, the heel small and sloping, and there are no accessory or cingulum cusps.

MOLARS.—On 47753 and 47808 the anterior molars are much worn, as they not infrequently are in pantotheres, the trigonid cusps being obliquely truncated. 47808, however, shows the structure very well in the middle and posterior molars, and it is chiefly from this hitherto undescribed specimen that the molar characters have been determined. The trigonid is unusually short and compressed antero-posteriorly. The pr^d is not slender as in *Amblotherium*, but rather broad and blunt—a condition even more strikingly displayed by the pa^d and me^d. The latter is shorter than the pr^d and is columnar, with rounded tip. The pa^d points more upward than forward, although it is not as high as the me^d, and seen from the internal aspect it has a subtle but distinctive subspatulate character. Below the sharp V-shaped notch between pa^d and me^d is a slight vertical furrow on the internal face of the crown, extending down to the point of root division. The narrow heel is of the usual triangular dryolestid type. The presence or absence of an external cingulum has not been ascertained.

Eight molars are present in 47808, of which the last is about as large as any which precede it, but a previous dissection of the side of the jaw reveals the fact that there were no more than these eight molars.

MANDIBLE.

The lower jaw of *Phascolestes* is closely similar to that of *Amblotherium*. The molar portion of the alveolar border is nearly straight, the more anterior portion gently concave. The lower border consists of a single convex curve from a point beneath the dental foramen to the anterior end of the symphysis. Below the dental foramen the curve becomes slightly concave and then passes posteriorly into another convexity which extends to the end of the angular process.

The symphysial surface is very long and slender, ending beneath P_3. The continuous, single, internal groove passes forward from in front of the dental foramen in a curve, concave upward, to the symphysis. The angular process is a slight, styloid projection directed posteriorly and not at all downward. On its inner surface begins the sharp but not high pterygoid crest which runs forward along the lower border, curving upward in front of the dental foramen, where it loses its sharpness, and passes into the anterior border of the coronoid. The posterior part of the mandible above the pterygoid crest is almost flat and featureless. The stout condyle is not supported by any definite internal thickening, and it is elevated far above the molar level. The articular surface faces rather upward than backward and is transversely elongated.

The anterior border of the coronoid arises at an angle of about 75° to the alveolar margin and is not thickened internally, the internal face of the coronoid not being excavated.

There is quite a marked difference in aspect between the anterior ends of 47753 (holotype of "*Amblotherium*" *mustelula*) and 47741 (holotype of "*Phascolestes longirostris*") which might at first sight seem to warrant specific differentiation. That of the former is of normal dryolestid type, while that of the latter is upturned in a most peculiar way, raising the incisors and canine well above the molar level. This must, however, be assumed to be due to *post-mortem* causes acting while the bone was still pliable (for it is not broken). The horizontal ramus is also somewhat deeper in this specimen than in 47753, but the difference is slight.

MEASUREMENTS.

	C.	P_3.	P_4.	M_1.	M_2.	M_3.	M_4.	M_5.	M_6.	M_7.	M_8.	M_{1-5}.
47753	—	—	—	0·7	0·9	1·0	1·2	1·2	—	1·0	—	5 0
47741	1·1	1·0	1·0	0·9	0·9	1·1	1·2	1·3	—	—	—	5·3
47808	1·1	—	1·0	0·8	0·9	1·0	1·1	1·2	—	1·0	0·9	5·0

Dryolestidae, incertae sedis.

(Pl. XI, fig. 7.)

The following specimens in the Beckles Collection from the Purbeckian of Durdlestone Bay, now in the British Museum, seem to be dryolestids, but are not more exactly determinable:

47770. Fragment of left ramus, outer aspect, with the canine (root divided) and impressions of the inner surfaces of the cheek teeth. Figd., as *Triconodon* sp. indet., Owen, 1871, pl. iii, fig. 20.

47795. Fragment of left ramus, external aspect, with posterior incisors and a small two-rooted canine and traces of the premolars, as well as impressions of the internal faces of the molars.

47803. Fragment of right ramus, internal aspect, with four fairly well preserved molars. Either *Phascolestes* or *Peraspalax*.

48244. Part of left maxilla with two badly broken molars. There is no median transverse ridge and the molars are very short and wide.

48401. Part of right ramus, internal aspect, with four broken molars. Perhaps belonging to *Amblotherium*.

48405. Left ramus, external aspect, with C, P_{1-4}, and M_{1-2}. This apparently represents a form not otherwise known, although it is too imperfect for detailed description. The premolars are low and long and each has a distinct anterior cusp as well as a posterior heel. The molars are of dryolestid type, with a faint external cingulum.

M 13132. Part of right ramus, with P_4 and three molars, internal aspect. This somewhat resembles *Phascolestes* but, so far as such fragmentary

material permits judging, the pa^d is more pointed and juts antero-internally to the me^d in an unusual way.

M 13131. Fragment of right ramus with a single broken molar, internal aspect. Probably an *Amblotherium*.

Pantotheria, incertae sedis.

(Pl. XI, fig. 8.)

The following indeterminate pantotheres are in the Beckles Collection in the British Museum and are from the Purbeckian of Durdlestone Bay:-

47769. Broken right ramus, internal aspect, with some fragments of teeth. Perhaps an amblothere. Figd., as *Triconodon* sp. indet., Owen, 1871, pl. iii, fig. 16.

47792. Left ramus, external aspect, with two molariform teeth and two elongated teeth in front of them which may be milk molars.

48208A. Canine with divided root. This is the tooth figured by Seeley (1893) as a reptile tooth. There can be no doubt that it is mammalian, and probably pantotherian, although it may be a deciduous triconodont canine.

48406. Right ramus, external aspect, with a premolar and the crushed germ of a molar. This somewhat resembles *Peramus*.

M 13133. Right ramus, internal aspect, with a premolar and two broken molars. This, too, might be *Peramus*.

M 13130. Angular process, with an impression of part of the rest of the left ramus. The angle is of the *Peramus* type, but the molar impressions do not seem to support this indication.

? *Pantotheria*, incertae sedis.

The following mammals, also in the Beckles Collection in the British Museum, and from the Purbeckian of Durdlestone Bay, cannot be identified at present:

47737. Apparently part of a right upper jaw with two teeth, a styloid one-rooted tooth and a somewhat compressed two-rooted one. Figd., as *Phascolestes dubius* Owen, 1871, pl. i, fig. 41.

47798. Fragment of a left ramus, external aspect, with one broken tooth, perhaps pantotherian.

M 13128. Fragment of a right maxilla, with a two-rooted canine. Possibly pantotherian.

ORDER MARSUPIALIA.

SUBORDER *POLYPROTODONTIA*.

FAMILY DIDELPHIIDAE.

GENUS EODELPHIS Matthew.

1916. *Eodelphis* Matthew, *Bull. Amer. Mus. N. H.*, XXXV, p. 482.

DIAGNOSIS.—Three lower incisors, the second enlarged, the others minute. No postcanine diastema. Anterior part of jaw deep and short. Trigonids moderately high, wider than long, protoconid about equal in height to the paraconid, metaconid lower.

GENOTYPE.—*E. browni* Matthew.

DISCUSSION.—The present genus is somewhat outside the scope of this monograph, being not only from a later horizon than any of the other forms described, but from a different continent—North America. It is, however, one of the most valuable Mesozoic mammal specimens preserved in Europe and the inclusion here of a brief note concerning it is convenient.

There can be little doubt that *Cimolestes cutleri* Smith Woodward and *Eodelphis browni* Matthew belong to the same genus. This genus is not *Cimolestes*, for, although the molars of the Belly River forms are very close to those of the Lance *Cimolestes curtus* Marsh, the latter species is not the genotype and was incorrectly referred to this genus. The earlier forms are therefore both referred to *Eodelphis* Matthew. *Eodelphis cutleri* and *E. browni* are closely similar and may be synonymous. They were described almost simultaneously from two mandibular rami, one a right and one a left, from the same formation and region. They agree very closely in size and in all comparable features. The only distinction not open to question is that in *E. browni* the mental foramina are slightly closer to the lower border—hardly a specific character. P_3 has a different aspect in the two, but it is badly worn and corroded in *E. browni*. The jaw of the latter is also a little more slender in the symphysial region, but the difference is hardly noticeable.

There are, however, marked differences in the molars as described by Matthew from those seen in *E. cutleri*. Matthew says that, in *E. browni*, the pr^d is lower than the pa^d and perhaps even lower than the me^d, and that pa^d and me^d are nearly equal on M_3 whereas the me^d is a little the smaller on M_4. In *E. cutleri* the pr^d is certainly taller than the me^d and probably overtopped the pa^d slightly, while on M_3 the me^d is definitely smaller than the pa^d. The type of *E. browni* has such badly worn molars that one may well expect further material to show that they were originally more like those of *E. cutleri* than the descriptions would indicate. For the present, however, both species must be retained. In the event of their proving to be synonymous *E. cutleri* has priority. It was first published May 30, 1916, and *E. browni* did not appear until July 24, 1916.

Eodelphis cutleri (Smith Woodward).

(Pl. XII, figs. 1–3.)

1916. *Cimolestes cutleri* Smith Woodward, *Proc. Zool. Soc.*, London, 1916, p. 525.

DIAGNOSIS.—Total length of cheek-tooth series about 30 mm. Differs from the supposedly distinct *E. browni* in the slightly stouter symphysial region, the position of the mental foramina farther from the lower border, and possibly in some details of molar structure.

FORMATION AND LOCALITY.—Belly River Series, Sand Creek, Red Deer River, Alberta, Canada.

MATERIAL.—The following specimen is in the British Museum:

M 11532. Part of right mandibular ramus with the crowns of P_3 and M_{2-3}, roots of P_{1-2}, M_1 and M_4 and alveolus for C. Holotype figd., as *Cimolestes cutleri*, Smith Woodward, 1916, fig. 1. (*Collected by W. E. Cutler*, 1914.)

DENTITION.

The incisive alveoli are broken away. The canine, judging from its alveolus, was very large and somewhat procumbent. P_1 was one-rooted, very small, and was crowded in between the canine and P_2, antero-internal to the anterior root of the latter. P_2 has two roots, the posterior one somewhat larger. P_3 is a large, heavy two-rooted tooth. The main cusp is stout, nearly circular in horizontal section and there is a much smaller posterior accessory cusp. Both cusps are now truncated by wear. The tooth is much heavier and less compressed than in the recent opossum. Its enamel is marked by slight vertical rugosities.

M_1 is absent and even its alveoli are largely broken away. M_2 is largely preserved but the trigonid cusps are badly worn. These cusps are only moderately worn on M_3 but the pr^d is broken off. The trigonid is much compressed antero-posteriorly. The me^d is distinctly smaller than the large, nearly erect pa^d. Judging from its base the pr^d must have been as large as the pa^d, or, possibly, slightly larger.

The talonid is broader than the trigonid at the base, although the distance across the apices of the cusps is less, while trigonid and talonid are of nearly the same length. Entoconid and hypoconulid are of about equal size on M_3 and are closely approximated, whereas on M_4 the entoconid is rather larger. The hypoconid is a stout cusp but somewhat lower than the other two. The heel is deeply basined.

There is a distinct, slightly nodulated anterior cingulum beginning at the antero-external angle of the base of the protoconid and rising rapidly toward the paraconid, which it does not reach. There is also a posterior cingulum passing from the postero-external angle of the base of the hypoconid upward to the apex of the hypoconulid.

M_4 is broken off, but it was at least as large as M_3.

Mandible.

The horizontal ramus is short and stout for a didelphid. A slight swelling beneath the anterior end of P_3 breaks the otherwise even curve of the lower border. There are two mental foramina, the larger one an elongated opening beneath the anterior end of P_3 and the posterior end of P_2, the smaller one beneath the anterior root of M_1. The masseteric fossa was deep, with a well-defined but rounded anterior boundary. The symphysis extends back to beneath the anterior end of P_3. Union was by ligament only. The pterygoid fossa is ill defined anteriorly.

Measurements.

	mm.
Total length of cheek series	29
Length P_3	5·5
„ M_2	4·5
„ M_3	5·2
Depth of ramus internally below the posterior root of M_3	11·2
Distance anterior mental foramen to lower border	3·5
Same, posterior foramen	4·0

SKELETAL REMAINS OF DOUBTFUL ORDINAL AFFINITIES.

Under this heading will be discussed several limb bones from the Stonesfield and Purbeck. Although undoubtedly mammalian, these bones cannot be assigned to any known genus or order, since the taxonomic system is based altogether on jaw fragments. Despite this unfortunate necessity of leaving them *incertae sedis*, the known limb bones are of outstanding morphological importance.

Femora.

(Pl. XII, figs. 5–7 ; Text-figs. 46–49.)

Material.—All the material is in the British Museum.

a. From the Stonesfield Slate at Stonesfield :

32752. A nearly complete right femur, seen in inferior aspect. Figd., Seeley, 1879, fig. 1. (*Presented by S. Peace Pratt, Esq.*)

b. From the Middle Purbeckian, Durdlestone Bay, Swanage, Dorsetshire. Beckles Colln. (*Purchased* 1876.)

48250. Right femur in anterior (superior) aspect.

M 13126. Right femur in posterior (inferior) aspect.

The Stonesfield Femur, 32752.

Morphology.—This bone is very peculiar, not closely resembling the corresponding part of any other known animal. The proximal end is widely expanded, both the trochanters being very strong. The greater trochanter extends externally from the condyle, as it does in most mammals, but the lesser trochanter, instead of

projecting somewhat ventrally, extends straight anteriorly (or mediad) opposite to the greater trochanter. The head of the femur is not supported by a definite neck, and its relationships to the shaft, and to the trochanters, are much as in *Ornithorhynchus*. The articular surface is not directed anteriorly or mediad and the normal position of the femur must have been nearly horizontal.

There is no digital fossa, but the intertrochanteric region is gently concave, somewhat as in *Ornithorhynchus*, although the concavity does not have as definite a lower limit as in the recent genus, but narrows and passes insensibly into a narrow and slight longitudinal groove which runs down the shaft. At the distal end this groove widens into the triangular popliteal fossa. This fossa is not deep and the bone at the bottom of it is irregular and rugose. The two condyles are poorly

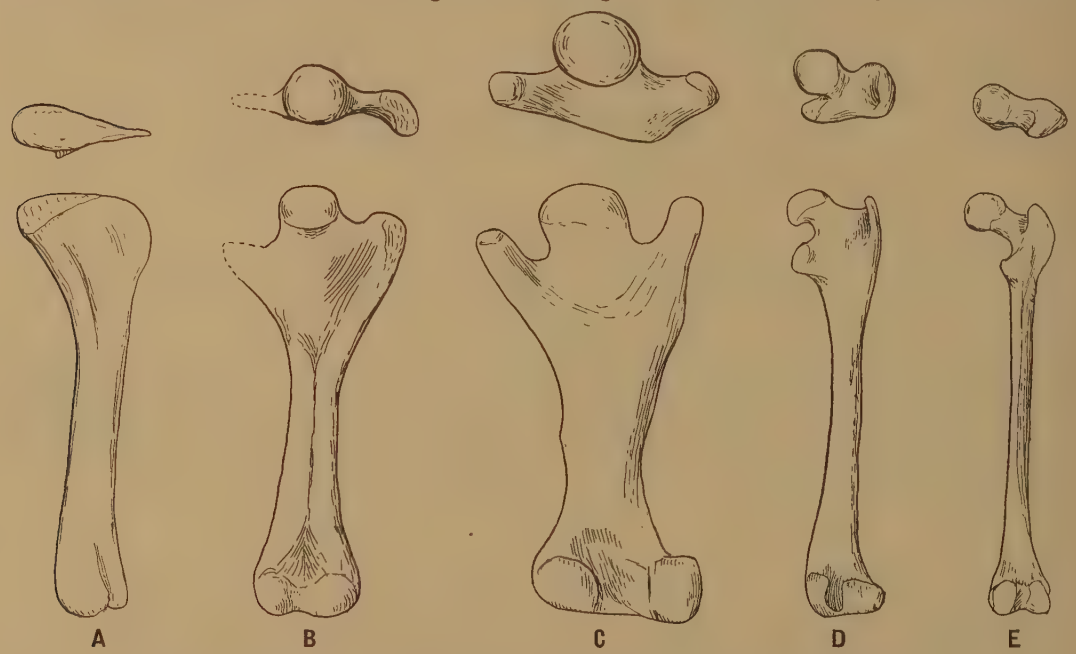


FIG. 46.—Comparative posterior or ventral views of right femora. A, *Microgomphodon*. B, Stonesfield mammal femur. C, *Ornithorhynchus*. D, *Didelphis*. E, *Homo*. Not to scale.

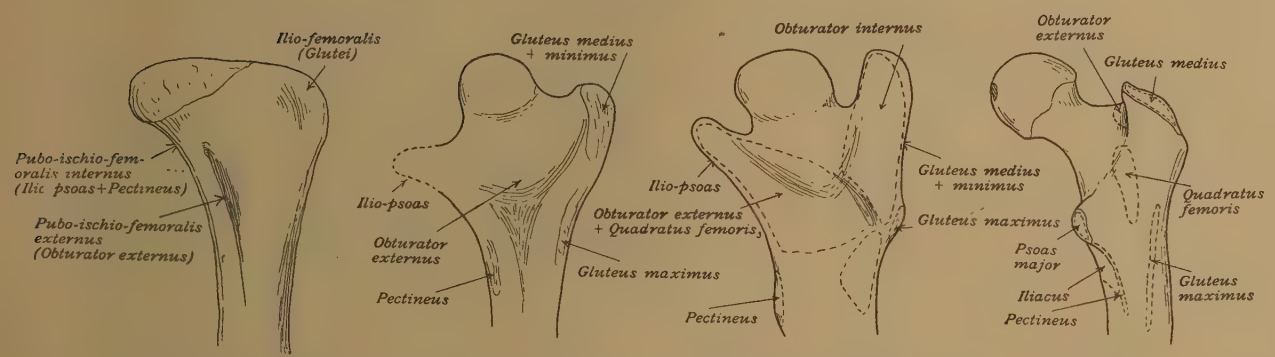
preserved, but were apparently of nearly equal size (the external a little the larger) and were well rounded.

The shaft of the bone is smooth and featureless save for the longitudinal groove already described, and for a slight ridge continuous with the distal border of the lesser trochanter and extending a short distance down the infero-anterior border of the shaft. Although not so massive as in *Ornithorhynchus*, the shaft of the bone is considerably stouter than in most later mammals of like size.

INTERPRETATION.—As very much the oldest known mammalian femur, this bone may be expected to throw much light on mammalian morphogenesis, especially on the homologies of the various structures seen in mammalian and reptilian femora. The trochanters of the femora of advanced mammal-like reptiles and of

primitive mammals may be tabulated as follows (based chiefly on Gregory & Camp and on Romer) :

	Muscle Insertions.	
Trochanter.	Mammal-Like Reptiles.	Mammals.
Greater tr.	Ilio-femoralis.	Gluteus minimus. Gluteus medius.
Internal tr.	Pubo-ischio-femoralis externus.	—
Lesser tr.	—	Ilio-psoas, Pectineus.
Third tr.	—	Gluteus maximus.
Fourth tr.	Caudi-femoralis. Ischio-femoralis. Pubo-ischio-femoralis posterior.	—



Microgomphodon | Jurassic Mammal | Ornithorhynchus | Homo

Fig. 47.—Posterior (ventral) aspects of the proximal ends of femora, showing muscle insertions. Not to scale.

The greater trochanter of the Stonesfield animal is thoroughly mammalian in character. It occupies the same position as the homologous element in the cynodonts, but is larger and is separated from the head by a distinct notch, never seen in the cynodont femur. The proximal external (or posterior) and externo-inferior border of the greater trochanter is roughened and undoubtedly served for the insertion of muscles homologous with the gluteus medius and minimus of mammals and with the ilio-femoralis of reptiles. The insertion of the gluteus maximus is seen in a somewhat broken ridge running distally from the greater trochanter. This ridge is homologous with the third trochanter, but is not developed into a definite trochanter.

As Romer has pointed out (1924) this femur strongly supports his theory that the reptilian internal trochanter disappears in mammals and that the lesser trochanter is a new structure derived from the insertion of the pubo-ischio-femoralis internus, originally dorsal, which moves to the internal or anterior border of the femur and becomes, in large part, the ilio-psoas. The internal trochanter served as

insertion of the pubo-ischio-femoralis externus, which becomes in large part the obturator externus and, in most mammals, moves in the same direction as the ilio-psoas (counterclockwise as the bone is viewed from the proximal end) towards the external (posterior) edge and proximally, finally being inserted in the digital fossa. In *Ornithorhynchus* the insertion is large and there is no digital fossa, and the same is true of the Stonesfield femur. It is worthy of note that there is in the femur of *Ornithorhynchus* a definite short ridge somewhat posterior to the position of the internal trochanter, as one would expect, and apparently homologous with the latter. Like the old reptilian internal trochanter, this ridge serves for the insertion of part of the obturator externus. In the fossil form, however, it does not occur.

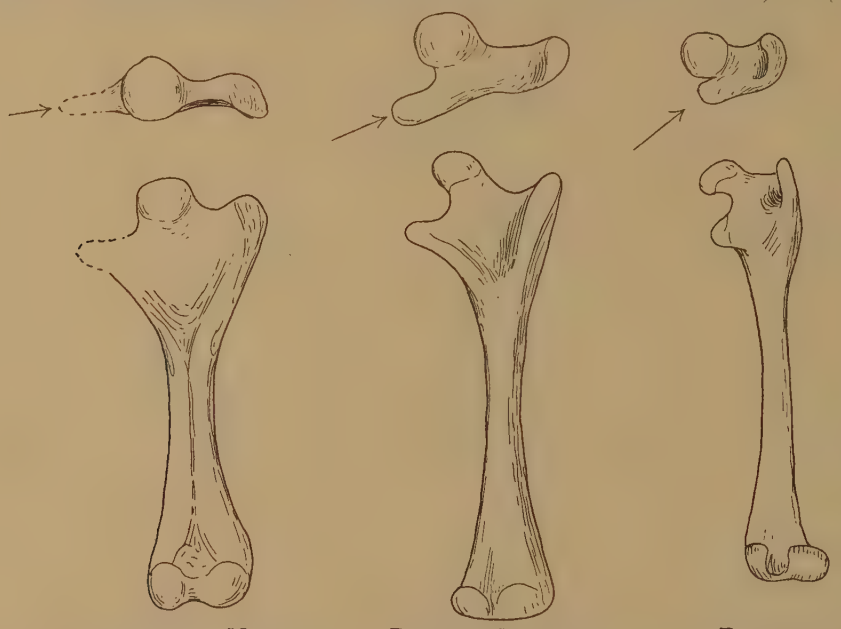


Fig. 48.—Posterior (ventral) and proximal views of femora, illustrating the migration of the lesser trochanter, indicated by an arrow in the proximal end views. From left to right, × 2 dia., × 4 diam., and × 1⅓ diam.

The Jurassic femur has a definitely mammalian lesser trochanter, but one which is in an extreme anterior position, notably nearer the position of the original dorsal reptilian homologue even than in *Ornithorhynchus* and very much nearer than in any other known mammal.

The ridge running distally from the lesser trochanter is clearly for the insertion of the pectineus, also derived from the reptilian pubo-ischio-femoralis internus.

The distal portion of the femur is not very characteristic. It avoids any of the specializations seen in later mammals and is quite suggestive of the reptilia in its rough and rather ill defined, subequal condyles.

Affinities.—The femur is of no detailed systematic value, as it is quite impossible to associate it with an established taxonomic group. It has, however,

been supposed to cast some light on the relationships of the Mesozoic mammals generally, as by Winge who mentions it and the associated humerus in support of his belief that all Mesozoic mammals were definitely monotremes.

The bone shows no signs of specialized marsupial or placental affinities, standing at a much lower level than any member of either of these groups. On the other hand, as Seeley pointed out, and as the above description has emphasized, the femur resembles that of a monotreme in many essential respects. It might even be described as a monotreme femur without the specialization seen in the recent forms; but the characters held in common must be admitted, in all probability, to have occurred in the ancestry of all known mammals. They do not indicate that the femur is that of a monotreme, but they do show that it is at a similar evolutionary level. It is prototherian, not necessarily in the sense of being a member of a natural group Prototheria, or of being related to the monotremes, but in an evolutionary sense, using the term prototherian to designate a grade of structure.

The Purbeck Femora (48250 and M 13126).

Description.—Two femora are known from the Purbeck and they seem to be essentially similar save that M 13126 is smaller and more slender. In this bone the head is lacking but its place of attachment is clear and its character is left in little doubt when it is compared with 48250 and two excellent American specimens of the same age and similar morphology. The greater trochanter is strong, somewhat longer antero-posteriorly in cross-section than it is wide transversely, and nearly erect. The lesser trochanter is also well developed, not at all erect as in *Ornithorhynchus* but projecting more nearly vertically from the shaft, as in the Stonesfield femur and most modern mammals. In direction it is almost ideally intermediate between the Stonesfield form and a primitive modern mammal. The inter-trochanteric area is developed into a moderately excavated fossa, deepest just mediad to the greater trochanter, although it does not here form a true digital depression.

Fig. 49.—Femora from the Upper Jurassic, middle Purbeck beds. A, right femur in anterior (superior) aspect, B.M. 48250. B, right femur in posterior (inferior) aspect, M 13126. Both × 4 diam.

The shaft is nearly circular in section, although the distal extension of the greater trochanter forms an angulation all the way down to the external condyle. The popliteal surface is but slightly excavated. The condyles are poorly preserved, but the external one was clearly larger and the intercondylar fossa appears to have been but slightly developed.

In 48250 the head and greater trochanter are both well preserved. The head

is borne on a definite constricted neck and is turned internally much as in primitive modern mammals (e.g. *Didelphis*). The greater trochanter is very stout and projects a little farther proximally than does the head. On its anterior surface is a somewhat roughened area, no doubt in part for the insertion of the gluteus minimus. The shaft of this specimen is somewhat stouter than that of M 13126 and is slightly rugose. The distal end is crushed. A rounded ridge extends proximally from the anterior part of each condyle, including between them a long triangular anterior depression, presumably continuous distally with the facies patellaris, but the limits of the latter cannot be made out. The lateral epicondyle is prominent, but the median slight, perhaps because of crushing.

INTERPRETATION.—The significance and great importance of the Purbeck femora is at once seen if they are compared with the Stonesfield femur on the one hand and that of a primitive recent mammal, such as *Didelphis*, on the other. The chief points that differentiate the recent form from the Stonesfield one are :

1. The head becomes supported on a definite neck and is turned at a definite angle to the shaft, in correlation with the bringing in of the knee toward the mid-line, under the body.

2. The greater trochanter becomes more erect, and a deep fossa is developed between it and the condyle for the insertion of the obturator externus.

3. The lesser trochanter moves ventrally or posteriorly.

In each of these respects the Purbeck form stands as an almost ideal intermediate between the earlier and the later one. The Stonesfield femur, as already pointed out, stands at a prototherian level. It is the most primitive known mammalian femur, representing the first stage after the quite distinct reptilian cynodont one. The recent monotremes have become somewhat specialized, but in essentials they have advanced little beyond this point. *Didelphis* is representative of a stage essentially metatherian in the evolutionary sense, which is primitive for both marsupials and placentals. Many lower placentals have femora not significantly different from that of the opossum. This stage was already reached in the Cretaceous, as specimens in the Yale Peabody Museum show. The Purbeck forms represent a transition intermediate between the two in morphology as well as in time, and show in a very clear way how the later form was derived from the earlier.

HUMERI.

(Pl. XII, figs. 4, 8 ; Text-figs. 50–55.)

MATERIAL.—The following specimens are in the British Museum :

a. From the Stonesfield Slate at Stonesfield :

M 13127. Nearly complete right humerus in posterior (median) aspect. Figd., Seeley, 1879, fig. 2. (*Presented by S. Peace Pratt, Esq.*)

b. From the Purbeckian of Durdlestone Bay, Swanage, Dorsetshire :

48361. Left humerus in dorsal (posterior) aspect, lacking the distal end, and the proximal end of a badly broken associated radius.

The Stonesfield Humerus (M 13127).

Morphology.—At first sight this humerus seems rather ordinary and would be taken for a somewhat stouter variant of the *Didelphis*-type. Closer study will reveal that it is entirely unlike any other known humerus whatsoever and is decidedly the most cynodont-like of known mammalian humeri, yielding nothing to the monotremes in this respect.

The head differs from that of the cynodonts, as also from that of the monotremes, in being nearly spherical. As in the cynodonts, there is no true greater tuberosity, the delto-pectoral crest passing insensibly into the rounded articular surface. The lesser tuberosity, again, is distinctly developed, as in the cynodonts, and is about as prominent as it is in later mammals generally. The shaft of the bone is

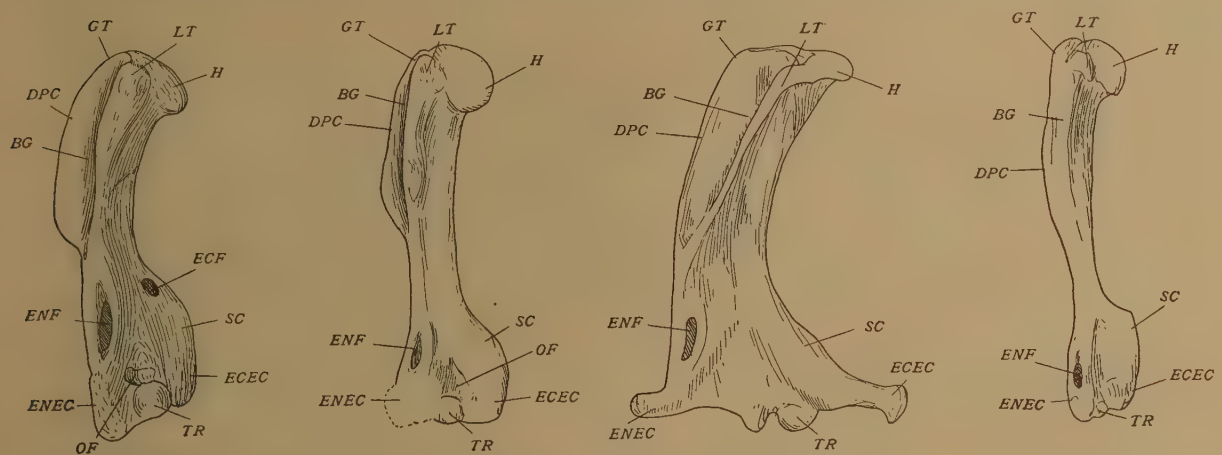


Fig. 50.—Median (posterior) views of right humeri. *BG*, bicipital groove. *DPC*, deltopectoral crest. *ECEC*, ectepicondyle. *ECF*, ectepicondylar foramen. *ENEC*, entepicondyle. *ENF*, entepicondylar foramen. *GT*, greater tuberosity. *H*, head. *LT*, lesser tuberosity. *OF*, olecranon fossa. *SC*, supinator crest. *TR*, trochlea. Not to scale.

rather straighter and relatively stouter than in cynodonts, and is much straighter and less angulate in section than is that of *Ornithorhynchus*. The division of the proximal part into triangular dorsal (posterior) and ventral (anterior) faces is obscured. The delto-pectoral crest is very prominent, nearly as much as in cynodonts, and extends more than halfway down the shaft. The ridge distal to the lesser tuberosity is more rounded, less high and thin, but is very distinct and ends distally, about two-fifths of the way down the shaft, in a distinct tuberosity (apparently for the latissimus dorsi and teres major insertions). The ventral face between these two ridges, the intertubercular fossa or bicipital groove, is relatively much narrower and shallower than in cynodonts and monotremes. It approaches the higher mammals in this respect. The proximal dorsal surface also shows some approach to the higher mammals in being large and much rounded. The distal end

is especially cynodont-like so far as preserved, presenting only very minor points of difference.

The relationship between the longer axes of the proximal and distal ends is of importance. In the cynodonts and their allies the angle between these axes (projected on to a common plane) is about 45° or even less ; in *Ornithorhynchus* the angle is about 80° ; while in most primitive marsupials and placentals it closely approaches or reaches 0°. In the Stonesfield humerus it is about 75°, greater than in cynodonts and about as great as in the monotremes.

The supinator crest is very like that of a cynodont, although perhaps a little less strongly developed, but the ectepicondylar foramen is absent, as in all mammals.

FIG. 51.—Diagram of posterior view of right fore-limb of the Stonesfield mammal to which the known humerus belongs, with probable arrangement of some of the more important muscles. Not to scale.

The olecranon fossa, which is rather broader and shallower than in cynodonts and in the later mammals with the exception of *Ornithorhynchus*, is subtriangular in shape. The entepicondylar foramen is large and is identical in position and character with that of the cynodonts. The entepicondyle proper is broken off, but from its base and from the mechanical relationships of the bone as a whole one is certainly not far wrong in restoring it essentially as in *Diademodon*, although it was probably a little weaker and certainly no stronger than in this reptile.

The radial and ulnar articulations are also extraordinarily reptilian. The true sharp-crested ulnar trochlea of later mammals is not well developed. The radius articulates on a separate rounded surface external and somewhat ventral to the ulnar articulation. There is no approach to the unique conditions seen in

Ornithorhynchus where the ent- and ectepicondyles are enormously developed and the radial and ulnar articulations are confluent, forming a single, somewhat twisted, subspherical surface with the radius articulating almost directly ventral to the ulna.

Posture.—The posture of the limb and the directions of the proximal and distal major axes of the humerus are closely related. In this form the angle between

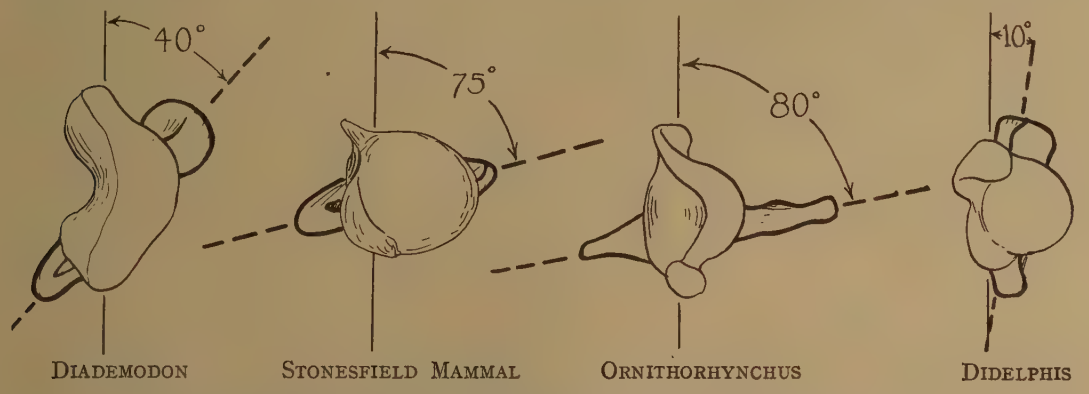


Fig. 52.—Proximal end views of humeri, to show the angles between the long axes of the two ends. The distal ends and their axes are drawn in heavy lines. Not to scale.

them is about 75°. The spherical head would suggest a position like that of the later mammals, as *Didelphis*, but this suggestion is certainly incorrect, for if the humerus is placed in this position the forearm is thrown almost horizontal and straight out from the body—an impossible position. Humeri in the position which is primitive for higher mammals, with the elbows drawn in towards the body, must necessarily have the axes of the ends nearly or quite parallel, bringing the point of

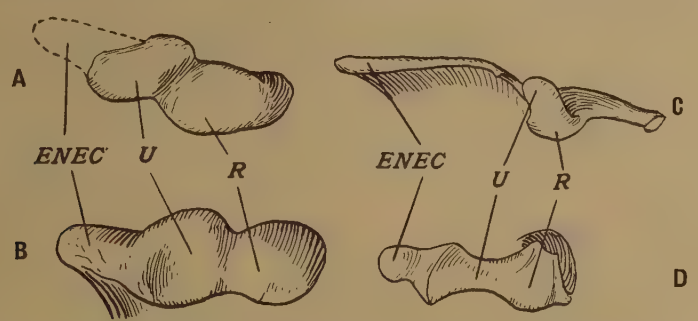


Fig. 53.—Distal ends of right humeri. A, Stonesfield mammal. B, *Diademodon*. C, *Ornithorhynchus*. D, *Didelphis*. Not to scale.

contact with the ground in under the point of support of the body and making the chief motion of both limb segments antero-posterior—the arrangement of maximum efficiency for a swiftly moving terrestrial quadruped.

It seems most probable that the normal position of the Stonesfield humerus was more or less horizontal, as in cynodonts and monotremes. The fact that the angle between the axes of the ends is much greater than in the cynodonts implies,

other things remaining the same, that the forearm was more nearly horizontal. This is the case in *Ornithorhynchus* and, as Watson has suggested, it has brought about the great expansion of the distal end in that form, counteracting the mechanical disadvantage of the horizontal posture of the forearm. This expansion has not occurred in the Stonesfield form, and we must assume that, concomitant with the rotation of the ends to a greater angle, there has taken place some other change which tended to counteract the effect of this on forearm posture. The only change which would bring this about is the rotation of the humerus as a whole in a clockwise direction,as seen from the distal end. This would necessitate a simultaneous change in the direction of the glenoid fossa. It is the more plausible since the lower end of the scapula points backward in both cynodonts and monotremes, and hence also probably in this Jurassic mammal, rather than forward as in higher mammals.

The rounded head indicates great freedom of motion at the shoulder, consider-

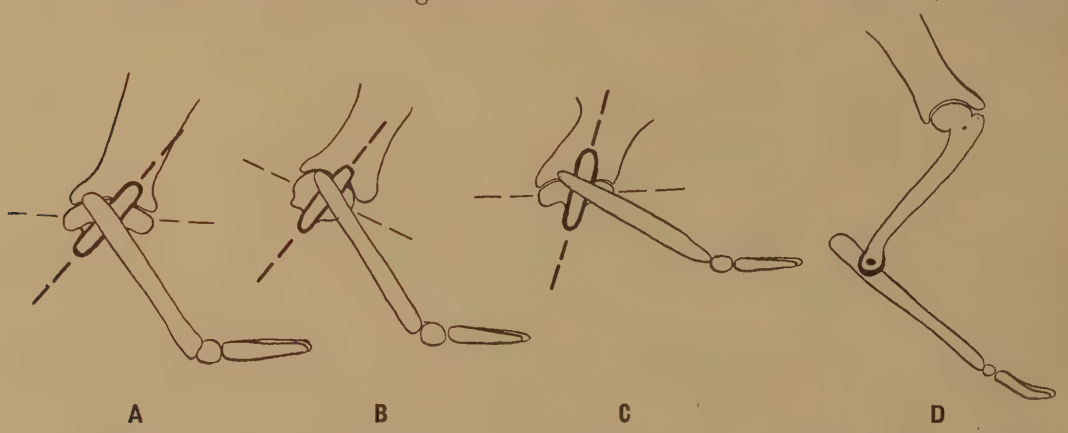


FIG. 54.—Diagram of lateral views of fore-limbs to show relationship between the axes of the ends of the humeri and the posture of the limb. The distal ends and their axes are in heavy lines. A, a cynodont reptile. B, the Stonesfield humerus. C, *Ornithorhynchus*. B, a higher mammal. Not to scale.

ably more than in cynodonts or monotremes. In the latter the motion at the elbow is unusually free, but that of the shoulder is rather limited.

AFFINITIES.—The Stonesfield humerus differs from a cynodont humerus essentially as follows :

1. Its head is spherical.
2. The inter-tubercular fossa is narrower.
3. The shaft is somewhat straighter and more definite.
4. There is a larger angle between the axes of the two ends.
5. The ectepicondylar foramen is absent.

All but the fourth of these are definite advances in the direction of the primitive marsupio-placental type.

The monotreme humerus is more like that of the cynodonts in the shape of the head, the wide, deep intertrochanteric fossa, and, to a lesser degree, in the character of the shaft, but it differs from them as follows :

1. The greater tuberosity is more distinct.

2. The shaft is stouter and more angulate.
3. The ectepicondylar foramen is absent.
4. The angle between the axes of the ends is greater.
5. The two epicondyles are extraordinarily produced.
6. Radius and ulna articulate on a single spherical facet.

3 and 4 are the only specializations shared by *Ornithorhynchus* and the Stonesfield mammal, but in the monotremes 4 goes hand in hand with 5, which is most different from the Jurassic form, and hence one must suppose the rotation of the ends in the two forms to be independently acquired. The only common specialization, then, is the very minor one of the loss of the ectepicondylar foramen, a feature common to all mammals and many reptiles, including some closely related to cynodonts. It is clear that the resemblances between the Stonesfield humerus and that of a monotreme, great as they are, are entirely due to inheritance of primitive features from a common ancestral reptilian stock.

Nor does it seem possible to derive the monotreme humerus from the Stonesfield one, for the living forms are less specialized in some features of the proximal end which are probably directly inherited from the cynodont stock. They are the shape of the head, the relationships of the two proximal crests, and the character of the bicipital groove. Hence the recent humeri and the Jurassic ones appear to be about equally advanced, from an evolutionary point of view, but they do not appear to be related. The Stonesfield humerus is rather less specialized. Its very primitive distal end contrasting with the highly specialized distal end of the monotreme humerus.

Except for the rotation of the ends (which is not sufficient of itself to bar it from the higher mammalian ancestry) the Jurassic humerus is an ideal prototype for those of marsupials and placentals, and shows a very distinct stage in the transition from the cynodont arm to that of a higher mammal. This does not mean that the animal to which this humerus belonged was necessarily ancestral in any direct way to any of the later mammals, although it may have been.

FIG. 55. — Left humerus in dorsal (posterior) aspect. B.M. 48361. × 3 diam. Upper Jurassic, middle Purbeck beds, Swanage, Dorsetshire.

THE PURBECK HUMERUS (48361).

This humerus lacks the distal end, and the proximal end is somewhat crushed and modified by pressure. The head is hemispherical, the lesser and greater tuberosities about equally developed. The delto-pectoral crest is very strong. It extends far down the shaft, and has a slight marginal dorsal ridge or tuberosity at a point about a third of the way from the proximal end. The ridge distal to the lesser tuberosity is like that of the Stonesfield form, shorter, less prominent, more rounded than the delto-pectoral crest, and ends in a small tuberosity.

Only enough of the distal end remains to make it seem probable that the angle between the axes was still large.

The humerus is very like that from Stonesfield and adds very little of interest. The presence of a distinct greater tuberosity is the only feature which can be considered as a definite advance.

The radius is a stout bone with a shaft nearly circular in cross-section. The proximal end is slightly expanded and its articular face is apparently concave and cup-like. It is badly crushed.

RELATIONSHIPS OF THE ORDERS.

In the last century there was a decided tendency, not yet quite outlived, to refer the Mesozoic mammals to the Marsupialia or to the so-called Metatheria, without special argument. The theoretical conceptions which have influenced the subdivision of the class Mammalia have often prejudiced the classification of these ancient and little-known forms, and still do so to an unfortunate extent.

The first writer fully to recognize the unique characters of marsupials and monotremes was de Blainville, who, in 1816, divided the mammals into two subclasses, the monodelphs and didelphs, the marsupials being normal didelphs and the monotremes anomalous didelphs, although the latter "perhaps ought to be made a separate subclass." This suggested step was taken by him in 1834 when he proposed the division of mammals into the subclasses of the monodelphs, didelphs, and ornithodelphs. In Gill's classification of 1872 these three great subclasses are recognized and are grouped as follows:

Mammalia	Eutheria	Placentalia or Monodelphia
		Didelphia
	Prototheria	Ornithodelphia

It should be noted in passing that the term "Eutheria" as originally proposed included both marsupials and placentals.

In his famous "Application of the Laws of Evolution to the Arrangement of the Vertebrata . . ." (1880) Huxley utilized Gill's terms and other analogous ones, but he used them in a very different sense. With Gill such a term as Eutheria was a taxonomic expression meant to include the members of a single, monophyletic natural group. With Huxley the terms Hypotheria, Prototheria, Metatheria, and Eutheria are designations for ascending *stages* in mammalian evolution. They are theoretical abstractions and not supposed phylogenetic units. Thus the Marsupialia are in a metatherian stage of evolution, but there is, following this system, *no* natural, monophyletic super-order or subclass Metatheria. The primates, for instance, are in a eutherian stage of evolution and they are, in Huxley's view, derived from an unknown group of metatherian primates, which decidedly does not mean that they are derived from marsupials. Similarly these metatherian primates, continuing to paraphrase Huxley, were derived, not from a primitive natural group of Prototheria, nor yet from monotremes, but from still more primitive *primates*, that is, from prototherian primates. Similarly with all the orders. The order Monotremata has not progressed beyond the prototherian stage, but that does not mean that it has any necessary connection with the hypothetical prototherian stages of the other orders.

These views of Huxley's are insisted upon, not because they seem tenable in the light of more recent study, but because they are almost universally misunderstood at the present time, and because the terms which he used are now used in several senses, without a clear understanding of the differences, and have been employed in the misclassification of the Mesozoic mammals.

Haeckel's views are typical of a large class, especially of recent zoologists, in the latter part of the nineteenth century. He adopts three sub-classes, the Placentalia, Marsupialia, and Monotremata, and he derives one from another in serial order. What is apparently done here is to confuse taxonomic groups and evolutionary stages, and this confusion was soon extended to Huxley's work and terminology. It is now very common, if not the rule, to see the subclass Eutheria derived from the subclass Metatheria, and the latter from the Prototheria, and to see Huxley quoted as the author of these views, although his own work shows that he would certainly have repudiated them in this form.

Is this not, in fact, simply a recrudescence of the old naïve conception of a *scala naturae*, masked by its application to great groups instead of small ones, and by its confusion of taxonomic and developmental terms, of the actual and the theoretical? Without entering into a discussion not wholly germane to the subject matter of this memoir, one may point out that more recent thought has tended away from this view, although the retention of the old theoretical subclass names often gives rise to confusion. Because there are three great groups of mammals to-day which exhibit varying degrees of retention of certain primitive characters, it most decidedly does not follow that they represent the survivors of so many natural groups of which each of the more advanced was derived from the one next less so.

It was this old misconception which long prejudiced the case of the Mesozoic Mammalia. It was felt, or even explicitly stated, that they must be marsupials because they are so ancient. Applying similar reasoning to smaller groups, it would be permissible to suppose that the more ancient of the known perissodactyls must all have been tapirs because the latter are, on the whole, the most primitive living members of the group. *A priori* considerations should enter into classification as little as possible, and there is no reason why a Mesozoic mammal should necessarily belong to an existing order, superorder, or even subclass unless a careful consideration of its known characters permits such an allocation. If modern knowledge of evolution permits any presumption, it is that mammals, such as the multituberculates, which appear at a time separated from the Tertiary by a span of more than twice the total duration of the latter itself, would hardly be expected to fit into a classification based exclusively on Tertiary and recent mammals.

The facts now available are not as extensive as one would like. It is not to be hoped that conclusions based on them will not require future modification, but at least they are adequate for the formation of reasonable working hypotheses. In forming these hypotheses an earnest effort has been made to base them on objective realities rather than on theoretical and preconceived beliefs regarding mammalian phylogeny, molar evolution, and so forth.

MULTITUBERCULATA.

It is probable that no other group of animals has given rise to such wide diversity of opinion regarding its relationships as has the order Multituberculata. They have been referred to each of the known mammalian sub-classes and to a distinct sub-class of their own. As to their more intimate relationships, at least ten or twelve mutually exclusive views have been expressed and warmly defended —this despite the fact that they are now rather well known, much better than any other group of Mesozoic mammals. Several fairly complete skulls are known, the dentition is clearly known in many forms, and parts of the fore-limb and almost the entire pelvis and hind-limb are known in typical members of the group.

The earliest expressed opinion was that of Falconer (1857 and 1862) who considered *Plagiaulax* as a marsupial closely related to the living *Hypsiprymnus*. Owen (especially 1871) agreed that it was marsupial, but very heatedly denied special affinity with the rat kangaroos. Gill (1872) placed the Plagiaulacidae as Marsupialia *incertae sedis*. Marsh (1880) gave the group ordinal rank, without denying the possibility of their being marsupials, and he later (1887) agreed that they were indeed marsupials. Cope (1884) considered them as directly ancestral to some or all later diprotodont marsupials, but when the teeth of *Ornithorhynchus* were described he decided that the multituberculates might be monotremes (1888). Osborn (1888A) in his memoir considers the multituberculates as a distinct marsupial sub-order to be definitely separated from the diprotodonts, although he grants the possibility of relationship to the monotremes. In his book of 1907 they form an order of doubtful affinities placed in the infra-class Ornithodelphia and sub-class Prototheria.

Gidley (1909), who had better material than any one who worked before him, agreed that the multituberculates were definitely marsupial and even revived the old conception of intimate relationship to the diprotodonts, although introducing a variation in this conception by supposing them to be an extinct side-branch from the ancestral diprotodont stock. Broom (1914), however, has shown that Gidley's evidence was inconclusive, and has advanced many good reasons for considering the multituberculates as monotremes, ancestral to the living forms. This paper is based on good material and the evidence is more fully and reasonably presented than anywhere else, so that this opinion is especially worthy of consideration. Winge (1923) also believes them to be monotremes, but apparently he does not consider them as directly ancestral to the living forms. Granger (1915), in a very brief abstract, has advanced the view that the multituberculates have nothing to do with recent mammals, but represent a distinct subclass. Finally may be mentioned the views of Ameghino (especially 1891 and 1903), by which the multituberculates become ancestral to diprotodonts, caenolestoids, and rodents ; of Hennig (1922), by which they become ancestral to monotremes and marsupials ; of Forsyth Major (1893 and elsewhere), who considered them ancestral to the rodents ; and of Hinton (1926), who would have them ancestral to all placental mammals.

Since the most widely accepted view for the past seventy years has been that the multituberculates are marsupials, it will be best at the outset to examine all the arguments advanced in support of this. They are listed below, with the name of the first or chief authorities to emphasize each :

1. The supposedly *Hypsiprymnus*-like shearing teeth. (Falconer.)
2. The supposedly diprotodont-like incisors. (Falconer, Gidley.)
3. The supposedly inflected angle. (Falconer and all subsequent supporters of this view.)
4. The character of the symphysial suture. (Falconer.)
5. The marsupial character of supposedly associated skeletal parts. (Cope.)
6. Supposed transition to true marsupials (caenolestoids) through the Polydolopidae and their allies. (Ameghino.)
7. Unequal development of fore and hind limbs. (Gidley.)
8. Fenestrated palate. (Gidley.)
9. Position of cheek teeth. (Gidley.)
10. General arrangement and function of teeth and development of skull and skeleton. (Gidley.)

The resemblance between the shearing teeth and incisors of multituberculates and some diprotodont marsupials is clearly convergent. Even the lower shearing teeth are not closely similar and are followed by teeth of very different type, and the upper shearing teeth of the two groups have no points in common. The development of procumbent incisors has taken place many times independently among mammals, and this is obviously the case here, for in multituberculates it is the second upper incisor which is hypertrophied, whereas in diprotodonts, as Osborn has pointed out, it is the first.

There is no inflected angle and the angular region is as different from that of the marsupials as it is from that of the placentals. It yields very strong evidence against reference to either of the higher sub-classes. Nor does the symphysis differ from that of any other mammal with similar mandibular characters.

The skeletal parts associated with the Multituberculata by Cope have since proved not to belong to them or to this group.

The problem of the relationships of the Polydolopidae and their allies is far too complex to discuss here, but it may be stated that after a prolonged analysis of all the evidence it is clear that the polydolopids are aberrant caenolestoids and have nothing to do with the multituberculates. The strangely multituberculate-like aspect of the jaw of *Propolymastodon*, as given by Ameghino and copied almost everywhere, is largely due to its being erroneously reconstructed. Gregory's conclusion as to the affinities of this group (1910) is found to be supported by all the evidence, both of the caenolestoids and of the multituberculates.

The seventh and ninth characters listed above, while they might, as Gidley affirmed, tend to indicate diprotodont affinities if the multituberculates were shown to be marsupials, obviously are not in themselves indicative of marsupial relationships. The eighth, the fenestrated palate, is not seen in *Tritylodon*, does not occur in all marsupials, and does occur in some placentals. If it were accompanied by

other marsupial characters it would be of important corroborative value, but, since it is the *only* definitely marsupial-like character of the multituberculates, its value is negligible.

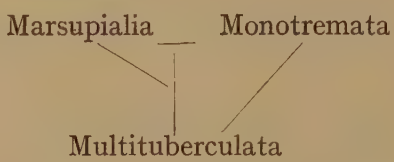
Finally, the tenth character listed is so general that only a general refutation can be entered against it. As is clear from a study of all the known material, and as will be further brought out to some extent below, there are no definitely marsupial characters in the dentition, in the skull, or in the skeleton of multituberculates. Such features as they do have in common with the marsupials they also have in common with other primitive mammals or with the cynodonts.

The actual evidence for this almost universal view of the marsupial nature of the Multituberculata is thus reduced by a full knowledge of the facts so far ascertained to a single character—the occurrence in most multituberculates of a fenestrated palate. This single and inconstant character is entirely insufficient to warrant so important a conclusion.

The theory that the multituberculates are related or ancestral to any, or to all of the placentals, has not been, and could not be, supported by any actual analysis of their characters. So far as published evidence goes, this view is based only on the belief that the ancestral placentals had many tubercles on their molars. Since the multituberculates do have many tubercles on their teeth (in most cases) it is argued that they represent those ancestral forms. The primary assumption of this argument regarding the ancestral molar is open to grave doubt if not, as most paleontologists (including the writer) believe, to actual refutation. Even granting this point, however, the conclusion is certainly unjustified, and does not follow. The multituberculates, clearly, could not be ancestral to any placental mammals. There is no detailed resemblance between the multituberculate molar and that of a rodent save the general one that both may have many cusps. No multituberculate has a canine, none has more than one lower incisor, none after the Triassic has more than two molars ; the premolars differ from the molars both in form and in function, and are very unlike any placental premolars. The lower jaw has no angular process. The skull roof and zygoma are highly specialized in a way which only superficially resembles the rodents and does not resemble any other placentals at all. The basicranium with its almost total absence of a postglenoid region is fundamentally distinct from that of any placental. The less plastic details of the limb structure give no suggestion of placental affinities. Only the name of the order supports this view, and that only if one grants the truth of the (at least) highly questionable polybuny theory.

Hennig's view that the multituberculates are ancestral to both marsupials and monotremes demands some consideration, if only because it is one of the most novel and recent conceptions and has not yet been discussed by other students. It follows, furthermore, a scholarly and detailed discussion of the Rhaeto-Liassic multituberculates of Germany for which all paleontologists are deeply indebted to Dr. Hennig. His conclusions may be freely translated as follows (1921) : " From the numerous statements, ever varying in detail, of contrasting relationships between multituberculates, polyprotodonts, diprotodonts, and monotremes, it is to be

concluded with a high degree of probability that these groups should be placed in a closed systematic unit. Broom especially has set forth, in a manner very convincing to me, the strong monotreme stamp in the structure of *Tritylodon*. Younger multituberculates show in essential features just as unmistakable relationships with certain marsupials. The only question left is, how far back one believes, or hopes, that the systematic division between marsupials and monotremes can be placed. . . ." This view is summed up in a diagram :



The placentals are, according to Hennig, independently derived from the so-called Protodonta.

The following considerations, among others, seem to disprove Dr. Hennig's contentions, which, it will at least be granted, call for much more evidence :

1. The identical tubercular-sectorial molars of marsupials and placentals are supposed to have been derived, quite independently of each other, from very different ancestral tooth-types.

2. The generalized marsupial dentition is derived from that of the multituberculates, despite the fact that the latter certainly could not, by any theory, be prototypal to such a dentition as, for instance, that of the opossum. The dental formula, if nothing else, should prevent such a view.

3. The only evidence of multituberculate relationships adduced is reference to the published work. It has been shown above that this work has not proved the marsupial affinities of the multituberculates. Even if it had, no worker on the group has ever considered it as possible that the multituberculates could be ancestral to all marsupials.

4. The very doubtful view is accepted that the multituberculate molar pattern is primitive.

5. Broom's conclusions seem to be misinterpreted, and they do not, in fact, support Hennig's view. Broom has specifically stated that it is the younger multituberculates which are monotreme-like, whereas the older ones (*Tritylodon*) are rather less so. The multituberculates may be paralleling or approaching a monotreme type, but it is very clear that they do not depart from that type and approach a marsupial-like one as this theory would demand.

6. Without any especial consideration of their compatibility two views are simultaneously advanced, despite the fact that those who published the data on which they rest all considered the two views as mutually exclusive.

Other facts might be noticed, but enough has been said to show that this theory cannot be adopted.

There are, in fact, only two conceptions of multituberculate affinities which our present knowledge of the morphology of this group permits us to consider

seriously. The first is the theory, so carefully and thoroughly supported by Broom (especially 1914) that they are ancestral monotremes, and the second is the view briefly mentioned by Granger that they represent a separate, extinct sub-class not ancestral or closely related to any later mammals. In the course of the following tabulation and discussion of characters the facts which have been, or can be, adduced in support or refutation of these two theories will be briefly mentioned.

I. Characters shared by multituberculates, cynodonts, and a number of primitive mammals :

1. Large vomer.
2. Palatine process of premaxilla.
3. Large nasals.
4. Septomaxilla (in *Tritylodon*).

II. Characters shared by multituberculates, cynodonts, and monotremes :

1. Supposedly uncoiled cochlea.
2. Supposed interclavicle.
3. Post-glenoid region very short, almost absent.

The characters listed under these two heads are simply primitive characters which give no index of special affinity. The presence of an uncoiled cochlea is quite probable, but cannot be considered as proven. In emphasizing the presence of an interclavicle, Broom relied on Marsh's assertions. The latter based himself on certain undoubted interclavicular fragments from the Lance formation, but so far there is no evidence that these really belonged to multituberculates. They may equally well have belonged to small reptiles, so that this feature is doubtful in the extreme.

III. Characters shared by multituberculates, some cynodonts, and many marsupials and placentals, but not by monotremes :

1. Large lachrymal in *Tritylodon*.
2. Three upper incisors.
3. Premolars present.
4. Molars functional throughout life.
5. Pterygoids largely vertical, not flattened.
6. Posterior nares between last molars.
7. Snout primitive.

These, also, are primitive characters and do not necessarily indicate special affinity. They do, however, show the absence of some very characteristic monotreme specializations.

IV. Character shared by most multituberculates, most marsupials, and some placentals :

1. Palatal vacuities.

As already suggested, this is the only character indicative of marsupial affinities, but it is of little value.

V. Characters shared by multituberculates and monotremes :

1. Lachrymal small or lost in later forms.
2. Frontals reduced and overlapped by parietals later forms.
3. Parieto-nasal contact in some later forms, sometimes even more marked than in monotremes.
4. Jugal small, on upper side of arch, or absent.
5. Squamoso-maxillary contact, known only in later forms but possibly present also in earlier ones.
6. Multicuspid molars, but see below.
7. No angular process on mandible.
8. Supraorbital foramina, known in *Djadochtatherium* only.
9. External auditory meatus not posterior to the glenoid cavity.

These are the only important items of evidence tending to connect the Multituberculata with any later order, and they are, with some additions, the characters relied upon by Broom when he advanced the theory that multituberculates are ancestral to monotremes. Their importance is indubitable, and certainly they show that many of the known characters of the multituberculate skull are monotreme-like. At the same time it is apparent that most of them are rather superficial and that the more fundamental monotreme specializations do not occur. Thus, the post-palatine region of the skull, whilst not as well known as might be wished, is clearly devoid of the monotreme peculiarities of this region. The extreme shortness of the post-glenoid part of the basicranium is, among mammals, very monotreme-like, but it is simply due to the retention of a cynodont character and is not a specialization indicative of affinity. In the placentals the post-glenoid region is very long, in the marsupials it is notably shorter, and in the monotremes, multituberculates, and cynodonts it is practically absent. The position of the external auditory meatus internal to the glenoid is a distinctly monotreme-like specialization, but it involves so little change from the cynodont condition that it cannot be very strongly relied on as an index of affinity.

The character of the mandible is also an important character, but its evidence is very equivocal. The multituberculate jaw is very unlike that of a marsupial or placental in its fundamental characters, and rather more like that of a monotreme. The likeness, however, consists chiefly in the absence of an angular process, a feature almost certainly inherited from the reptilian ancestry and not due to a specialization common to monotremes and multituberculates. The specializations of the multituberculate jaw are very unlike those of *Ornithorhynchus* and even less like those of *Echidna*. The short, stout symphysis, the great pterygoid flange, the strong masseteric crest, the upstanding coronoid process—all are very unlike the monotremes. Even taking into consideration the undoubted degeneracy of the jaws of the living forms, it is clear that the mandibles yield no valid evidence of close affinity. If anything, they indicate that the relationship is remote at best.

The first five characters listed above are of a more superficial nature. Each of them may be found paralleled by other mammals, although their association

does bring about a definite but perhaps misleading resemblance to the monotremes.

The teeth are so much better known than any other feature and are such generally useful indications of relationships that special emphasis must be laid on them. Cope claimed the teeth of *Ornithorhynchus* as multituberculate, and this view has been widely accepted, although Osborn has pointed out that actually these teeth do not resemble those of the Multituberculata at all closely (1907, p. 107). We may go farther and show that the monotreme teeth, degenerate as they are, furnish definite evidence *against* derivation from the Multituberculata. The teeth of *Ornithorhynchus* are not really multicuspid but bicuspid. They consist essentially of two large cusps, external in the lower jaw, internal in the upper. Between and around these cusps, and from them to the other side of the tooth, the surface is flattened or more or less basined, and the edges of the tooth are much crenulated. These crenulations are small and do not deserve to be considered as true cusps. They are clearly secondary, analogous to the cuspules invariably developed on a somewhat degenerate crushing tooth, *e.g.* in the bears or arctocyonids. They do not mask the original bicuspid, interlocking nature of the molars. Indeed, except for having many cuspules, as have the teeth of pigs, mastodonts, many carnivores, many caenolestoids, diademodonts, and numerous other animals which obviously have attained them independently, the *Ornithorhynchus* molar has no points of resemblance to that of any multituberculate. The emphasis on two marginal cusps, the reversed character of upper and lower teeth, and their interlocking relationships are not degenerate but ancestral characters of the monotreme molars, and they are entirely unlike anything seen in multituberculates. The numerous cuspules are not ancestral but secondary, and are, in any event, different in form, arrangement, and function from the cusps of the multituberculate molars. The character of the molars of *Ornithorhynchus* not only does not support the hypothesis that this animal is a descendant of the Multituberculata, but it makes that view highly improbable.

VI. Characters peculiar to multituberculates.

1. Never more than two molars in plagiaulacoids; never a canine; early complete loss of all but one lower incisor, and enlargement of second upper incisor.
2. Entirely unique molar pattern.
3. Early high specialization of premolar pattern and function.
4. Form of the posterior part of the mandible.
5. Humerus of eutherian aspect, but unique in details.
6. Pelvis and hind limb of peculiar and quite independent type.
7. Unique enamel structure.

Their dental characters alone are enough to exclude the multituberculates from the ancestry of any later group, nor do they seem to have been derived from any known mammalian type. Even in the Triassic, long before the appearance of any non-multituberculate mammals, the tritylodontoids had highly specialized and

very characteristic molars. The history of the plagiaulacoid molar is fairly well known. It begins with a simple, six-cusped, two-rowed type and is complicated by the addition of cusps to each row and the addition of a new row of cusps in the upper molars, the cusps themselves meanwhile acquiring a definite and rather intricate ridge pattern. The earliest plagiaulacoids, as also the tritylodontoids, have molars as unlike those of the primitive contemporaneous mammals of other orders as is well possible. Beginning with a different heritage, evolving in a distinctive way, the multituberculates achieve a final dental type entirely peculiar to themselves.

The mandibular morphology has already been mentioned. It is fundamentally distinct from either the marsupials or placentals, almost equally so from the monotremes, and finds its only close comparison with the triconodonts and symmetrodonts.

The skull does not present any important known characters that are unique, although the observed combination of characters is very distinctive.

The limb structure, and especially the structure of the pelvis and hind-limb, is of great importance. This rests chiefly on Gidley's publication of some important fragments in the United States National Museum (1909) and on a very nearly complete hind-limb in the American Museum of Natural History, not yet described in full (Granger, 1915). It is not possible to go into detail in this place, but the conclusions based on this material may be stated. The limb structure seems on the whole definitely more progressive than that of the monotremes and is metatherian from an evolutionary (but not taxonomic) point of view. It could not have given rise to the prototherian limbs of the monotremes. At the same time it is very distinctive and is neither marsupial nor placental in type. Granger's conclusion, that the limb structure indicates that the multituberculates have no close relationship to any of the existing sub-classes, seems the only one warranted by the material.

An important new line of evidence on mammalian relationships has recently been developed by Dr. J. T. Carter. In his researches, of which only a small part has yet been published, he has been able to show that the minute structure of the enamel of mammalian teeth, especially as revealed in etched thin sections, furnishes a reliable general index of affinities. Fortunately he has been able to examine the enamel of some of the younger multituberculates (1922), with the result that their enamel is found to be very characteristic and quite distinct from that of any other known vertebrates. This very definite evidence relative to a character which is demonstrably inadaptive and not subject to convergence must be considered as of the first importance.

If one weighs the remarkable multituberculate peculiarities, and considers the potentialities which they have shown, as well as the clearly recorded course of their history in the Upper Jurassic, Cretaceous, and Paleocene, it is impossible to avoid the conclusion that they represent an independent, specialized group. They have only the remotest relationship with any later mammals, perhaps (as their geological distribution and dental morphology, especially, would indicate) being independently derived from the reptiles. They certainly are not marsupials or ancestral to any marsupials, nor can they possibly be considered as placentals. If related to any

living mammals, it is to the Monotremata, but the evidence for this view is inconclusive and there is very strong evidence against it. They cannot reasonably be placed in any of the major taxonomic groups of the class Mammalia, and therefore Marsh's name Allotheria may conveniently and appropriately be retained as a designation of more than ordinal rank for the group to which the Order Multituberculata is to be referred.

If it is felt that this endows a little known Order with too great a dignity, it may be remembered that even in the present imperfect state of knowledge there are known twenty-four or twenty-five distinct genera, that the Order was world-wide in distribution, and that its recorded history extends over a span greater than that of any other order of mammals.

TRICONODONTA.

Opinions as to the relationships of the Order Triconodonta have been pleasingly unanimous. Except for that of Winge (1923), there appears to be no significant classification which does not, with varying degrees of confidence, refer the triconodonts to the Marsupialia or Metatheria (in a systematic sense). As this conclusion rests entirely upon the analyses of Owen (1871) and of Osborn (1888A), the evidence as given by the latter may first be summed up and discussed :

1. " Mylohyoid " groove present.
2. Angle inflected and " fully marsupial in *Triconodon.*"
3. Incisors primitively four, reduced to three.
4. Premolars usually four and their mode of reduction supposedly marsupial.
5. " Mode of . . . succession strikingly marsupial."
6. Supposed family likeness of the Triconodontidae to the Dasyuridae.

Osborn concluded at that time that there was " no reasonable doubt as to their relationship " to the marsupials, and that " the Triconodontidae were undoubtedly in the marsupial line." Nevertheless as we review the evidence to-day not a single item of it is valid :

1. The internal groove finds a possible homologue quite as often in the other mammals as in the marsupials, is by no means constant in the latter, or even certainly present in any case.

2. The Triconodonta have no angle, inflected or otherwise, and this region is quite unlike that in any group of recent mammals.

3. The incisor number is inconclusive, being comparable to that in cynodonts and, presumably, similar in the ancestry of all mammals.

4. Premolars are never four in number in any known marsupials, whatever may have been the condition in their ancestry, whereas they are often four in placentals and may be reduced in the same way as in the Triconodonta.

5. The only evidence of succession rests on a single specimen, which shows both the canine and the last premolar being replaced, a most un-marsupial replacement, while there is no good evidence that the other premolars and incisors were not also replaced.

6. As Professor Osborn would be the first to claim to-day, the resemblance between the Triconodontidae and Dasyuridae is entirely superficial, and that the latter are derived from polyprotodonts with tuberculo-sectorial molars quite unlike anything in the ancestry of the triconodonts.

It thus proves, most unexpectedly, that this view of triconodont relationships has remained almost unchallenged for over a hundred years without anyone advancing a single valid item of evidence in support of it.

The only definite facts given by Winge to support his reference of the triconodonts (and all other Mesozoic mammals) to the Monotremata were, first, that he recognized the non-marsupial and non-placental character of the jaw and compared it with that of *Ornithorhynchus;* and, second, that he considered knowledge of tooth change to be too incomplete to serve as valid evidence of marsupial affinities. Both these facts are quite true, but they certainly do not form an adequate basis for referring the triconodonts to the Monotremata.

Both Winge and the upholders of marsupial relationships have unquestionably been influenced by their belief that it was possible to trace a transition from the Triconodonta to the Pantotheria. By Winge the Jurassic mammals, excluding multituberculates, are divided into three groups. In the first the molars have three cusps in a single series and there is no angular process on the mandible. In the third there is an outer cusp as well as the three inner ones on the molars and there is an angular process. The second group was supposed to be transitional between these two and to have only three cusps on the molars, as in triconodonts, but to have an angular process, as in his Amblotheriidae. This group, to which he gave the name Amphilestidae, does not exist. As has been shown above, *Amphilestes* itself is a typical triconodont and has no angular process or any other transitional character, while of the other forms placed here, *Amphitylus* is the same as *Amphitherium* and *Dicrocynodon* and *Docodon* are actually the most specialized of known pantotheres, with fully opposed molar cusps, basined heels, and other specialized characters, and without any approach to the triconodonts.

The other supposed transitional series between triconodonts and pantotheres was first emphasized by Osborn and has been widely, but by no means universally, accepted. He divided his Triconodonta into three groups, the first with the cusps in a straight line, the third with the lateral cusps strongly rotated inwards, and the second transitional between these unlike extremes, with the lateral cusps on the inner slopes of the central cusp. Here, again, the supposedly transitional group does not really exist. One member, *Phascolotherium*, is a true triconodont with the cusps as nearly as may be in a straight line. The other member, *Tinodon*, is really a typical member of the third group; indeed it is synonymous with a genus which Osborn himself referred to the third group. The triconodonts and symmetrodonts are fundamentally dissimilar, and transitional types do not occur. Even if this were not true, there would be another difficulty for, as will be shown below, the supposed transitional stages between symmetrodonts and pantotheres also are non-existent.

The actual known characters of the triconodonts will be tabulated and discussed.

I. Primitive characters not indicative of special affinity :

1. Presence, at most, of four incisors, four premolars, and five molars.
2. Retention of the canine in all forms.
3. Known characters of the brain.
4. Uncoiled cochlea.

These characters have a certain value in so far as they indicate the absence of various specializations diagnostic of other groups. Thus in retaining (*e.g. Amphilestes*) five molars, reduced to four or three in later forms, they differ from both marsupials and placentals ; in having four premolars they are seen to be without a universal and very characteristic marsupial specialization ; and in retaining, at least in some forms, four incisors they differ from the placentals. These points, however, cannot be stressed except in this negative manner, for the presence of four incisors, four premolars, and a greater number of molars was undoubtedly characteristic of some stage in the ancestry of both marsupials and placentals.

The characters of the brain and of the cochlea in *Triconodon* are different from those of any other known mammal, but, again, they undoubtedly are very close to an ancestral condition otherwise unknown.

II. Character shared with most multituberculates, most marsupials, and some placentals :

1. Fenestrated palate.

As in the case of the Multituberculata, this equivocal character is the only one at all suggestive of marsupial affinities.

III. Characters shared with multituberculates and monotremes and rarely or never seen in the more primitive marsupials and placentals :

1. No jugo-lachrymal contact.
2. Jugal reduced.
3. Lachrymal reduced or wanting.

Although not primitive for placentals and marsupials, each of these characters may, of course, appear in those groups. Furthermore, although the jugal is reduced, it is not much like that of the multituberculates and monotremes, and is not confined to the top of the zygoma.

IV. Characters shared with monotremes and with no other orders :

None.

V. Character shared with symmetrodonts and multituberculates :

1. Condition of the angular region.

The character of the posterior part of the mandible is one of the most important of the few osteological features known for this group, and in it the triconodonts stand rather close to symmetrodonts and multituberculates. Its most characteristic feature, however, is largely negative, and is probably part of the reptilian and not of the mammalian heritage. While it is of importance in separating the triconodonts from the angulate mammals—marsupials and monotremes, it is insufficient, by itself

and in the face of much contrary evidence, to indicate a possible union of the non-pantotherian Jurassic mammals in a natural group.

VI. Character shared with placentals and, to a less degree, with marsupials, but very different from the monotremes and multituberculates:

1. Elongation of the basicranium posterior to the glenoid.

This specialization, which involves deep-lying readjustments of basicranial structure, very strongly opposes close relationship of the triconodonts to the multituberculates, or to the monotremes, in which the basicranial alterations lead not to a loss but to an accentuation of the extreme posterior position of the glenoid seen in the cynodonts. We do not yet know exactly how these cranial readjustments were made in the triconodonts, and it is probable that they were quite distinct from those seen in the marsupials and placentals. This character cannot now be considered as good evidence in favour of relationship to either of the latter.

VII. Chief characters peculiar to triconodonts:

1. Tooth pattern.
2. Character of the palate.
3. Basisphenoid.

The basisphenoid, as described in this work, and the palate, as described in an earlier paper (Simpson, 1925A), are unique, and considerable importance must be attached to them. The few osteological characters known for the triconodonts exhibit a rather confusing morphological eclecticism. Together with features peculiar to themselves they unite characters resembling those of several other groups, with a result that their general morphology is altogether unique. Relationship to any one group of later mammals is not indicated, and it would manifestly be absurd to regard the triconodonts as related to all the orders which they resemble in one character or another.

As usual, the evidence of the teeth is here worth more than the few other known facts together. The history of the triconodont molar teeth is clearer than that of any other known type. In the Upper Jurassic is found its highest possible development, the genus *Triconodon* itself, with the three cusps equal in size and a very strong and characteristic shearing action. In the Middle Jurassic are found forms in which the midcusp is much the largest, and one of them would serve very well as a structural ancestor for the Upper Jurassic ones. In the Triassic are found cynodont reptiles, such as *Ictidopsis* or *Microconodon*, with teeth which are very close to those of the Middle Jurassic mammals, but with the anterior and posterior accessory cusps still smaller. In the Permian are found related carnivorous reptiles with the accessory cusps absent and the teeth consisting only of a compressed main cusp. It is impossible to doubt that one has here the actual structural stages of the evolution of the triconodont molar. At no time in its history does the triconodont molar resemble that of any other primitive mammal, and the supposed transitional types tending to bridge the gap between triconodonts and symmetrodonts or pantotheres do not exist. The fact that some placentals (especially some seals and fissipeds) and marsupials (*Thylacinus*) resemble the triconodonts in molar

pattern has nothing to do with the case. The resemblance is not close, the mode of occlusion and mechanics of use are different, and the later forms are manifestly secondary and derived from a tuberculo-sectorial type, while the true triconodont pattern is manifestly primary and has nothing to do with the tuberculo-sectorial type.

The triconodont pattern is also very distinct from that of the multituberculates, although the work of Watson on the origin of the diademodont molar shows that multituberculates and triconodonts possibly had a common ancestor. In justice to him, however, it must be mentioned that Professor Watson does not himself make this application of his discoveries among diademodont molars. Certainly any common ancestor must necessarily have been very remote and *reptilian*, not mammalian.

Nor is there any sure ground for associating the triconodonts and the monotremes, although, despite appearances, there is more fundamental resemblance between the triconodont molar and that of *Ornithorhynchus* than between the latter and the multituberculate molar. Both *Triconodon* and *Ornithorhynchus* have in the molars a single longitudinal row of main cusps with a cingulum or shelf, narrow in *Triconodon*, wide in *Ornithorhynchus*, which may be crenulated in both cases and which is internal on the lower molars, external on the upper. This is too slender a resemblance to support an hypothesis of relationship between the two groups, but it does indicate a very simple and sound way in which the monotreme molar may have arisen, and it helps to emphasize the fact that it cannot have arisen from the true multituberculate type.

To sum up all the evidence as it now stands:

1. The triconodonts certainly were not marsupials or placentals.

2. There is no valid evidence tending to connect them with the monotremes and there is some good evidence against this view.

3. They represent, in all probability, an unsuccessful independent side-branch of the Mammalia not related to any later forms.

4. There is a possibility that a remote, reptilian ancestry was common to them and the Multituberculata; but the evidence for this view is inconclusive.

SYMMETRODONTA.

The symmetrodonts are the least known of all Mesozoic mammals. They occur only in the Purbeck-Morrison, and even there are very rare. The lower jaw and lower dentition are, however, fairly well known in three quite distinct forms, and a good upper dentition of one genus and a single upper molar of another are available. Opinions as to relationship must, even now, rest almost entirely on the dentition, as has been the case in the past.

Owen separated *Spalacotherium* from the triconodonts and placed it among the pantotheres. Marsh made a distinct family Spalacotheriidae for *Spalacotherium* and *Menacodon*, but he began the confusion which has long existed between triconodonts and symmetrodonts by making a family Tinodontidae to include *Tinodon* and *Phascolotherium* (1887, p. 340). Osborn (1888A and 1907) adopted exactly the

same grouping, but included these groups as subfamilies of the family Triconodontidae. This view has carried the field and is now almost universally held, although the only three workers who have made a thorough review of the evidence have all expressed doubts concerning it. Thus Gregory (1922) questions the inclusion of *Spalacotherium* and its allies in the Triconodonta and calls them pseudotrituberculates, while Matthew (in Gregory, 1922, pp. xiii, xiv) believes them entirely distinct from the Triconodonta and would refer them to the "Tuberculata" (Pantotheria), and I have advanced reasons for considering them as a distinct order not at all related to the Triconodonta but perhaps distantly related to the Pantotheria (Simpson, 1925D). This latter view is strongly supported by the English material, the only difference being that the relationship to the Pantotheria seems to be a little closer than was considered probable on the basis of the American material alone.

In the form of the mandible symmetrodonts do show considerable similarity to the triconodonts. The form of the coronoid is distinctive and the condyle is placed at a higher level, but the condition of the angular region is much the same. As has been noted, this is largely a negative character which cannot be too strongly relied upon to unite the triconodonts and symmetrodonts, but which must be considered as very gravely hindering the connection of the latter with pantotheres, marsupials, or placentals.

If the symmetrodonts are actually to be derived from the triconodonts, it follows, as Osborn has well shown, that the symmetrodont type must have arisen by the rotation inwards of the anterior and posterior accessory cusps of the triconodont type. The evidence for this view may be abstracted as follows :

1. In *Phascolotherium* the lateral cones are said to be slightly internal to the main one.

2. It is said that *Tinodon* and *Menacodon*, while on two different lines of descent, represent progressive advances in the internal shifting of the cones.

3. These genera are further said to be more primitive than *Spalacotherium*, but to lead to it structurally.

None of these arguments is valid :

1. *Phascolotherium* is a true triconodont and does not, in fact, show any cusp rotation.

2. *Tinodon* and *Menacodon* are not progressive stages but are identical, *Menacodon* being a synonym of *Tinodon*, and *Tinodon* does not, in fact, approach *Phascolotherium* in molar structure.

3. *Tinodon* is quite distinct from *Spalacotherium*, and it is, on the whole, quite as specialized. Certainly it makes no closer an approach to the triconodont type.

The evidence for cusp rotation is not good, and it is probable that the antero- and postero-internal cusps of the symmetrodont molar arose where they are now found. The survival in the Upper Jurassic of the almost unicuspid *Amphidon* molar type, with the accessory cusps faintly indicated on the slopes of the main cusp, seems to support this view.

The mechanical relationships of the triconodont and symmetrodont molars

are also very different. The triconodont lower molars shear upward and inward against the upper molars, whereas the symmetrodont type is interlocking and triangular and the shear is not like that of the triconodonts but is more scissor-like.

It is concluded that the symmetrodont dental type is, as Matthew has already stated, fundamentally distinct from that of the triconodonts. It is next necessary to consider its relationship to that of the pantotheres.

There are some important similarities which lead one to conclude that they must be related in some way, thus :

1. In both orders the molar teeth are triangular and interlocking.

2. In both the chief action in biting is that of a scissor-like shear along two oblique cutting edges.

3. In both the internal apex of the upper molars, and the external apex of the lower molars are most emphasized.

The differences, however, are more numerous and important :

1. The symmetrodont molars are nearly symmetrical, the pantothere molars markedly asymmetrical.

2. The symmetrodonts have no talonid and no trace of having possessed one in their ancestry, whereas the pantotheres all have distinct talonids articulating with the protocones.

3. The symmetrodonts always have internal cingula on the molars and the accessory cusps seem to be derived from the slopes of the main cusp, whereas the pantotheres never have internal cingula and the accessory cusps appear to be derived from the basal part of the tooth.

4. In the symmetrodonts the lesser cusps of the upper molars are along the anterior and posterior borders, and there are no cusps along the external border, whereas in pantotheres there may be a large centro-external cusp and the chief cusps (except for the internal one) are always on the outer border. Pantothere upper molars are also generally more transverse.

It has been thought that the transition from the Symmetrodonta to the Pantotheria could be traced through such an undoubted pantothere as *Asthenodon*, which was supposed to be without a talonid and to approach *Spalacotherium* rather closely. It now appears, however, that "*Asthenodon*" has a well-developed heel of the Dryolestid type, that it is, in fact, a synonym of *Dryolestes* itself. There are no transitional forms between the cingulate, non-heeled symmetrodonts and the non-cingulate, heeled pantotheres.

The symmetrical nature of the symmetrodont tooth is not so much to be emphasized as was believed by Gregory (1910) and, formerly, myself. The molar of *Spalacotherium* is not absolutely symmetrical, although it is much more nearly so than that of any pantothere, and although even in this genus the antero-internal and postero-internal cusps are of the same size and nature, which is not quite the case with any pantothere.

The different relationships of these internal cusps in the two groups may indicate that they are not homologous, although this cannot be rigidly proven. The upper molars have a certain similarity, both being triangular with the highest cusp internal,

but otherwise they are quite different. The decided difference in the angular region of the lower jaw must also be remembered.

It is concluded that the symmetrodonts form a distinct order of Mesozoic mammals allied to the pantotheres by way of a rather remote common ancestry. The question of their relationships to post-Mesozoic mammals is thus intimately connected with that of the pantotheres. It is clear, however, that they represent an aberrant side-branch of mammals which was tending away from the ancestry of marsupials or placentals while the pantotheres were tending toward this ancestry. The symmetrodonts have no diagnostic marsupial or placental characters.

PANTOTHERIA.

The first Mesozoic mammal described was a pantothere, and the first expression of opinion as to pantotherian affinities was, appropriately enough, that of Cuvier, who considered *Amphitherium* as " quelque Didelphe." The essential point of this identification was not shaken for well over fifty years. In 1871 Richard Owen implied that in some of the pantotheres the marsupial characters were little differentiated from the modern insectivorous types. Nevertheless he considered them all to be marsupials and even saw in *Amphitherium* the prototype of *Myrmecobius*, although *Stylodon* figures as the prototype of *Chrysochloris*. Marsh (1880) in defining the order Pantotheria stated that its generalized members " were doubtless the forms from which the modern specialized Insectivores and Marsupials, at least, were derived,"—a view essentially similar to that of Owen. Later, however, Marsh retreated from this strong standpoint and omitted the words " and marsupials " from the passage quoted (1887). At this time he supposes the Allotheria to represent the Mesozoic marsupials and the Pantotheria the Mesozoic placentals. Looking back after forty years, it seems that Marsh's original views of 1880 were much nearer the truth than those of 1887, which, patently, were influenced by contemporaries whose first-hand acquaintance with the evidence was not equal to his own.

In his memoir (1888A) Osborn divided the pantotheres into two sharply distinct groups, referring one group to the marsupials and one to the placentals, but in 1888B he recognized the essential unity of the order and since that time he has considered the group as placental.

Winge (1923) has referred the Pantotheria to the Monotremata, along with all the other Jurassic mammals, but most palaeontologists have followed one of the two chief lines already laid out, either referring the order to the Placentalia or else considering it of less than ordinal rank and placing it among the Marsupialia Polyprotodontia. Only Gregory (1922) has supported the view hinted at by Owen and adopted, but later abandoned, by Marsh that the Pantotheria represent or are related to the common ancestry of placentals and marsupials.

In considering the relationships of the Pantotheria to other, and especially to later, mammals, the problem is placed, even at the outset, in quite a different light from that of the other Jurassic orders. In the other groups the molar patterns and general characters are very much unlike those of any later mammals, and it

was necessary to consider whether these groups were related at all closely to Tertiary or recent ones. It has been decided after a review of the available evidence that they were not. In the present case, however, it is immediately apparent that a relationship must exist. The following rather summary list indicates the inevitability of such a view as the very basis of discussion :

1. General arrangement of tooth series as in primitive marsupials and placentals.
2. Premolars very close in pattern to those of the most primitive later mammals.
3. Lower molars with a distinct but very primitive tuberculo-sectorial pattern.
4. Upper molars triangular in contour (although not in structure) and representing a stage from which those of later mammals could be derived.
5. Mandible of a type which could readily be prototypal to those of later mammals.

This list could be greatly extended, but it suffices to show that the pantotheres certainly are related in some way to later mammals. The question to be decided is whether they are ancestral, as an Order, to any or all later mammals or represent an extinct offshoot, and, in either case, whether they are more closely related to the marsupials or to the placentals, or whether they may not be related to both equally?

Winge's opinion that the pantotheres were monotremes is hardly worthy of serious consideration. The only evidence which he gives is, first, that they appeared to him to be related to the triconodonts; and, second, that their resemblance to *Myrmecobius* was secondary and not indicative of close affinity. In the second he was certainly quite correct, but this does not make the pantotheres monotremes. As regards his first, it has already been shown that his supposed group intermediate between triconodonts and pantotheres does not exist and that, even if it did, there is no good evidence that the triconodonts were monotremes. The pantotheres do not have even one character definitely suggestive of monotreme affinities.

The following arguments have been advanced, from time to time, in support of placing the pantotheres among the Marsupialia :

1. Resemblance to the triconodonts (Osborn, 1888A, Gregory, 1910).
2. Resemblance to *Myrmecobius* (Owen, etc.).
3. Supposed inflected angle of *Amphitherium*.
4. Broad coronoid.
5. Manner of reduction of premolars (Osborn, 1888A).
6. Number of molars usually greater than three.
7. Two-fanged canines (Osborn, 1888A).
8. Incisors more than three, at least in some cases.
9. Supposed resemblance of *Kurtodon* to *Phascolomys* (Osborn, 1888A).

These may be discussed in the same order :

1. The triconodonts and pantotheres do not, in fact, share even one feature which is not either inherited from the reptiles or else included in a minimum definition of the class Mammalia. They show no sign of special relationship within the class. Even if they did, it would not make the pantotheres marsupials, since the triconodonts are not marsupials.

2. The only resemblance to *Myrmecobius* which is not also a resemblance to almost any primitive later mammal lies in the high number of molars in the latter. But recent studies have shown that this character is not ancient but new, and that this genus is derived from a group with not more than four molars. The molar form in *Myrmecobius* is not like that of the pantotheres and is degenerate.

3. The angle of *Amphitherium* is not inflected, nor is that of any pantothere.

4. This is not an exclusive or even typical marsupial character.

5. This is based on the most specialized pantothere and one certainly not ancestral to later forms (*Dicrocynodon*). It is not proved so far as regards the marsupials themselves. As a matter of fact pantotheres have typically four premolars, very seldom fewer, while marsupials with more than three are unknown.

6. This and 8 are the only valid items of evidence, but even these lose all their force when it is remembered that cynodonts also have a greater number of incisors and of molars and hence that reduction must have taken place somewhere in the ancestral placental line.

7. Two-fanged canines are neither characteristic of, nor confined to, marsupials.

8. See 6.

9. As Osborn later recognized, there is no real resemblance between *Kurtodon* and *Phascolomys*.

There is thus no good evidence of special marsupial affinities. The evidence for placental (insectivore) affinities is as follows :

1. *Chrysochloris*-like crowns and occlusion of *Asthenodon* (Osborn, 1888A).

2. More generally, the resemblance of dryolestid lower molars to those of the zalambdodonts.

3. Upper molars broad transversely and short antero-posteriorly.

4. Incisor series longitudinal.

5. Four premolars.

6. Distinct, non-inflected angular process.

Of these it may be noted :

1. This was based on a misconception of the characters of *Asthenodon*.

2. The very different detailed structure of the upper molars, among other things, shows that this is due to convergence.

3. This also is probably secondary and convergent in part, although rather short wide molars are probably primitive for both marsupials and placentals.

4. Correlated with the jaw form and also seen in long-jawed marsupials.

5. Most anatomists now agree that the remote marsupial ancestor must also have had four premolars.

6. The non-inflected angle is the strongest item of evidence in favour of placental affinities, but it is not a decisive one. The non-inflected angle of the cynodonts, the occurrence of a non-inflected angle in a marsupial, and the occurrence of an inflected angle in some primitive placentals, all indicate that such evidence must be taken with care. The first fact, especially, permits one to believe that the angle of the marsupials was probably non-inflected at some remote time, while the last two show that an inflected angle may be derived from a non-inflected one.

There is, then, no decisive evidence as to placental affinities either. If pantotheres were necessarily one or the other, there would be, perhaps, some reason for referring them to the placentals rather than to the marsupials; but, as has been shown, there is little or no positive evidence for this view. The pantotheres are, in fact, remarkably free from those peculiarities which later developed in the marsupial and placental lines and which enable one to distinguish them so readily at the present time.

The following characters of the Pantotheria are common to the primitive placentals and marsupials or are such as must have occurred in the ancestry of both:

1. Dental formula primitively one which could give rise to that of any later mammal by reduction.

2. Incisors styliform, more or less procumbent, serial in arrangement.

3. Canines enlarged, somewhat recurved, often two-rooted.

4. Premolars all two-rooted, sharply differentiated from molars, with a high piercing cusp and low posterior heel, and last premolars generally higher than first molars.

5. Lower molars of very primitive, four-cusped, tuberculo-sectorial type. Upper molars of type which, by stages indicated by actual specimens in the Cretaceous, could give rise to the primitive tritubercular type of placentals and of marsupials.

6. Mandibular rami long and slender, little divergent, with long cartilaginous union at symphysis.

7. Coronoid often high and broad. Condyle slightly above alveolar level. Angle small, but with condylo-angular notch much more definite than in cynodonts. Angle not inflected.

It would next be in order to list those features common to the various pantotheres which would not be found in the common ancestry of the marsupials and placentals. There are none. Generic and familial specializations occur which would, of course, exclude most of the known forms from the direct line. The dryolestids show rather clear evidence of secondary shortening of the molars, with modifications of the talonid and reduction of the outer part of the upper molars, more advanced in some than in others. The dicrocynodonts have gone off on a tangent of premature and fruitless specialization. It would indeed be an almost unbelievable coincidence if the very few pantotheres known to us happened to include a member of the limited group which actually gave rise to the marsupials and placentals. It is from the characters of the order as a whole, the characters which seem clearly to be primitive for its own members, that its affinities are to be judged. *Amphitherium*, indeed, has no known characters which would exclude it from the ancestry of any later pantothere, marsupial, or placental. Further knowledge of this mammal might necessitate some modification, but there can be no doubt that it is altogether unique in its prototypal morphology. The paurodontids, while they represent a side line, show how the marsupial or placental stock was probably derived from the Amphitheriidae. They change the ancestral molar type very little, but they exhibit marked reductions in the dental formula. Reduction having set in, it was carried beyond the point found in ancestral placentals or marsupials.

To sum up; on the basis of the facts now known, and without making a futile attempt to discount the future, it may justly be said that the pantotheres show no features which would indicate exclusive relationships with either marsupials or placentals, that they exhibit no characters which would exclude them from the ancestry of either group, and that, in the known parts, they display, as an order, all the characters which would necessarily appear in the common ancestor of marsupials and placentals. The characters involved are too many and too intricately co-ordinated for this to be mere coincidence or convergence, and the only conclusion possible at the present time seems to be that the Order Pantotheria does represent the ancestry of both marsupials and placentals, without itself belonging to either group.

CRETACEOUS MAMMALS.

Between the Upper Jurassic mammals and the next youngest known there is a great gap which can at present be filled only by inference. Upper Cretaceous mammals belong to three well-defined orders. The multituberculates continue, evolving in their own way, but triconodonts and symmetrodonts are not present. Nor are the pantotheres present as such, this stock being now represented by insectivores and didelphids. The placental and marsupial lines are now quite distinct. The conception that the Jurassic and Cretaceous mammals are ordinally related, and that no great break exists until the end of the Cretaceous, is quite untenable. Although it is clear that they could have been derived from the Pantotheria, even the very early forms from the Djadochta formation of Mongolia are no longer pantotheres, but definite insectivores.

MONOTREMATA.

Of the history of the monotremes before the Pleistocene nothing whatever is known from actual specimens. "*Xenotherium*" Douglass *non* Ameghino (= *Epoicotherium* Simpson) was believed by Douglass to be a possible North American Oligocene monotreme, but re-study shows that this certainly is not true and that *Epoicotherium* is a primitive subterranean edentate. *Desmostylus* Marsh from the Miocene of North America and Japan has been hailed by Abel (1923) as a descendant of the multituberculates and an ancestor of the monotremes, but examination of the originals of the photographs on which Abel based his view shows that some of the supposed resemblances between these forms do not exist and that the rest are entirely superficial. *Desmostylus*, indeed, can have nothing to do with either multituberculates or monotremes, and there is every reason to accept the original view of Marsh, supported and expanded by Hay (Proc. U.S. Nat. Mus., XLIX, p. 381), that it is an aberrant sirenian.

Ameghino has described a number of bones from Patagonia which he referred to the Monotremata, but he too was certainly mistaken.

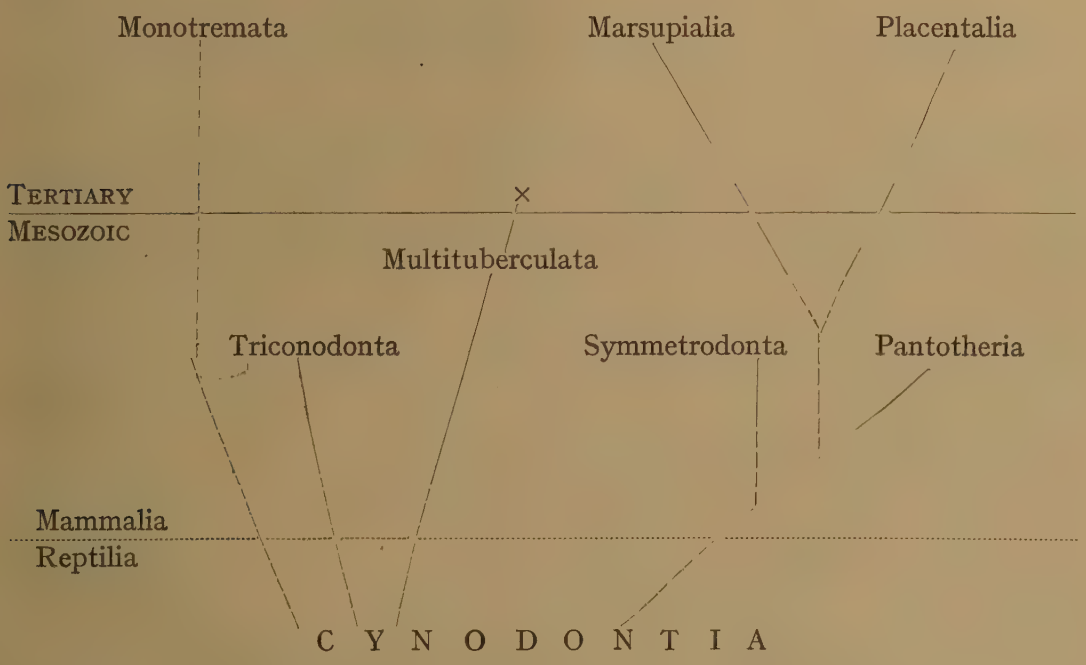
Nor do ancestors of the monotremes appear in the Mesozoic, despite the fact that most of the Mesozoic mammals have at one time or another been referred either to the Monotremata or to the Prototheria. *Thlaeodon* Cope from the American

Cretaceous was at one time considered a monotreme, but Matthew has shown that it is a didelphid. That none of the Jurassic orders have any close affinities with the Monotremata has been shown above, so that the ancestry of this group has yet to be discovered. It is probable that it was quite distinct from all other mammalian orders from a very remote time, or even that it was independently derived from the Reptilia.

There is nothing really remarkable in this lack of ancestral monotremes. Throughout the Tertiary, and perhaps for some time before that, the group has probably been Australian, and the pre-Pleistocene mammalian life of the Australian region is still virtually unknown. The known Mesozoic mammals are extremely few in number, and the chances in any event would be strongly against any of them being related to a small and isolated group like the Monotremata. Even in the Mesozoic Era Asia would be the most probable place to look for ancient monotremes. Only five species of Mesozoic mammals are known from Asia, and these are from well up in the Cretaceous.

Summary.

The following table gives the relationships of the various groups of mammals in accordance with the conclusions reached in the previous pages:



STRATIGRAPHY.

Rhaeto-Lias.

Of the three groups of mammals from the Rhaet-Lias only the English ones are exactly determinable as to horizon. These are from two localities, *Hypsiprymnopsis* from near Watchet, and Moore's collection from near Holwell, both in Somersetshire. The geological and other circumstances of these finds are given in Moore, 1867, Dawkins, 1864, and Richardson, 1911. The latter divides the English Rhaetic as follows:

Rhaetic
- Upper
  - Watchet Beds
  - Langport Beds
  - Cotham Beds
- Lower
  - Westbury Beds
  - Sully Beds

The Westbury beds are the black *Pteria contorta* shales. They contain the Rhaetic bone-bed at or near their base, although the horizon does not seem to be invariable and more than one bone-bed may occur. In most regions the lower limit of the Rhaetic is at about this level and is quite definite, the Sully beds and more or less of the black shale being absent; but at Watchet the Sully beds are well developed. They are definitely separated from the Westbury beds and their upper surface is channelled, indicating a non-sequence. The term Sully beds, as used by Richardson, includes only the upper part of the so-called grey marls, the lower, non-fossiliferous part, although conformable with the upper, being linked with the tea-green marls of the Keuper. The Sully beds, which may vary from 0 to 14 feet in thickness, thus belong to the very base of the Rhaetic.

It was in these beds and at a depth of 10 feet 6 inches below the basal bone-bed of the Westbury beds that Dawkins found *Hypsiprymnopsis*. It occurred in place on the wave-cut platform between low- and high-water levels west of Watchet and was, according to Dawkins, associated with *Acrodus minimus*, *Sargodon tomicus*, *Gyrolepis alberti*, *G. tenuistriatus*, a pterosaurian bone, part of a pen of *Belotеuthis* or *Geoteuthis*, a small amphicoelian vertebra, a few fragments of wood, and *Pecten valoniensis*. Other Rhaetic guide fossils, especially pelecypods, which have been found in these beds leave no doubt that they are correctly separated from the Keuper. The Rhaetic section west of Watchet is given in great detail by Richardson, from whom the following is borrowed in very much abbreviated form:

COAST SECTION AT BLUE ANCHOR POINT.

Lower Lias.		Hard blue shattered limestone. Shales .. .. Limestone, sometimes inconspicuous		1′ 0″
Upper Rhaetic.	Watchet Beds.	Shales and marls with a few thin limestone bands		7′ 7″
	Langport Beds.	Alternating beds of limestone and marl from 1″ to 7″ thick ..		2′ 3″
	Cotham Beds.	Shales with two limestone bands	3′ 10″	5′ 4″
		Massive limestone, with 3″ of marl at the base	1′ 6″	
Lower Rhaetic.	Westbury Beds.	Black shales and black or dark limestones		23′ 8½″
		Bone bed		0′ 6″
		Black shales and grey or dark limestone, with a little irregular sandstone near base		22′ 4″
		Basal bone-bed, with lumps of Sully marl		2′ 0″
	Sully Beds.	Grey to dark marls		13′ 1″
Keuper.		Grey, greenish-grey, to black marls, with gypsum.		

The horizon of *Hypsiprymnopsis* is about 2½ ft. above the Keuper as the line is drawn by Richardson in this section.

Conditions near Holwell, where all of Charles Moore's specimens were obtained, are very different, the Rhaetic being represented only by the Westbury beds, as shown in the following section (from Richardson) :

MARSTON ROAD SECTION, HOLWELL.

INFERIOR OOLITE.	Limestone, hard, dense, conglomeratic at base	2′ 0″	*Acanthothyris spinosa, Terebratula globata, Syncyclonema demissa, Isocardia* sp., *Trigonia* sp., *Ostrea* sp.
	Non-sequence.		
LIAS.	Limestone, hard, whitish, sparry, pebbles of pure limestone (Langport Beds?) at the base, top portion considerably bored by *Lithophagi*	Variable in Thickness.	
	Non-sequence.		
RHAETIC. (Westbury Beds.)	Limestone, somewhat sandy and earthy, with fragments of Carboniferous limestone ..	0′ 4″	*Acrodus minimus, Gyrolepis alberti,* and vertebrae.
	Shale, yellow, gritty, calcareous	0′ 6″	Full of fragments of *Pteria contorta, Chlamys valoniensis* and *Protocardia.*
	Breccia in intermittent patches, firmly adherent to the Carboniferous limestone ..	0′ 2″	Usual fish remains.
	Unconformity.		
CARBONIFEROUS.	Carboniferous limestone, presenting a very irregular surface.		

The surface of the Carboniferous limestone was exposed to subaerial erosion for a long time and the surface is much corroded, great fissures being developed in places. These fissures communicated with the surface in lower Rhaetic time, and when the sea invaded the area they were filled with debris. It was from one of them that Moore's collection of mammal teeth was procured. These are apparently to

be assigned to the same age as the Westbury beds, and thus are younger than *Hypsiprymnopsis*, although still in the lower Rhaetic. The associated fauna is almost identical with that in the Württemberg bone-beds, and is also remarkably like that of Stonesfield in facies. There are fragments of reptiles, marine and terrestrial, very abundant remains of fishes (selachians, ganoids, and *Ceratodus*) and some marine invertebrates, almost exclusively pelecypods. From the fissure which Moore explored so thoroughly he obtained twenty-nine mammal teeth, nine species of reptiles, and fifteen of fishes. There were about 70,000 teeth of *Acrodus* alone.

No mammals are known in England between the Lower Rhaetic and the Bathonian. The German Mesozoic mammals, on the contrary, belong to the Upper Rhaetic or even to the Liassic, although it is not possible to determine their age with exactitude. For only one or two of them is the precise locality known, and even in these cases the age remains somewhat uncertain.

All are from the "Rhaetic bone-bed"—a determination which was once considered sufficiently exact as to horizon, but which now proves to be singularly unsatisfactory. Recent studies of the Rhaetic of Württemberg (see especially Hennig, 1922, 1923, and Ehrat, 1920, where many further references will be found) have shown that there is not one bone-bed at one horizon but that there are many, each being lenticular (although often of considerable extent), and that the horizon may vary from Upper Keuper to Lower Liassic, while two or even three bone-beds may occur at different horizons in the same section. This naturally necessitates exact field data for each find, an unmixed collection of associated fossils, and other information totally lacking in the case of the known teeth of *Thomasia*, *Tritylodon fraasi*, and *Oligokyphus*.

The conditions of deposition are summed up as follows by Ehrat:

"Ueber das absinkende Land ingredierte sich das sehr seichte Rhätmeer in einer flachen, schmalen SW-NO verlaufende Strasse, an welche einzelne Buchten und Ausläufer sowie in manchen Gebieten flachsumpfige Gelände sich anschlossen. Nur an wenigen Stellen lebte eine reichlichere vorwiegend aus Lamellibranchiern bestehende marine Fauna. Flüsse, welche vom vindelischen Rücken herabkamen, häften ihr Material in Form von Deltabildungen nach Art der submarinen Flutfazies auf. Aeolische Kräften mögen dabei eine gewisse Rolle gespielt haben, jedoch dürfte es zuweit gegangen sein wenn R. Lang die ganze Rhätformation als äolmarine Bildung auffassen will. Das Auftreten der Sandsteine in einzelnen Inseln, der Wechsel von Sanden in Tonen, das rasche Auskeilen und die unregelmässige Schichtung in der Nähe der Küstenlinie erklären sich am Besten durch solche Deltas, wo der Absatz der Sinkstoffe weniger regelmässig ist und meist in nur feinerdige Stoff abgelagert werden, die weit im Meer hinein verbreitert werden können."

The deposits are those of a shallow sea in the immediate vicinity of the coast, and the fossils are mostly those of such superficial waters or of the land itself. Fishes and marine reptiles are fairly common, land animals are relatively rare. The last labyrinthodonts occur, while *Phytosaurus*, *Plateosaurus*, pterosaurs, and the mammals also speak of the proximity of land. There are ichthyosaurs, nothosaurs, plesiosaurs, numerous sharks, especially *Hybodus*, two species of *Ceratodus*, and five ganoids.

The invertebrate fauna is almost entirely composed of lamellibranchs, especially the zone fossil *Avicula contorta*, while cephalopods, corals, and sponges are absent.

The bone-bed itself is largely a conglomeration of coprolites (which won for it the unpleasant name of " schwabische Kloake " from Quenstedt), teeth, scales, etc. With regard to its age Ehrat says, " Wir sahen, dass unser Bonebed nicht etwa einem durchgehenden Horizont entspricht ; vielmehr kann es sich überall einschalten, bald an der unteren Grenze, bald im Verband der Rhätsandsteine, aber auch über denselben als Grenzschicht, sowie im untersten Lias. Die Bezeichnung ' Grenzbreccie,' welche Plieninger für dies Bildung einführten, trifft insofern nicht für jedes Bonebed zu, als es keineswegs immer die Grenze zwischen dem obersten Rhät und untersten Lias bildet und somit also Grenzhorizont nicht zu verwerten ist. Auch möchte ich es nicht mit Endlich ' markante Schicht ' als abschluss des Keupers ' bezeichnen. . . . Vor allem wäre es falsch, wollte man jedes Bonebed unsere Horizonte als rhätisch betrachten. . . ."

As for the position of the particular bone-beds from which mammals have been derived, Lörcher has found the bone-bed to be Liassic near Olga-hain, whence came at least one and perhaps two of the mammals. Ehrat says of this locality, " Beim Olgahain findet man an mehreren Stellen anstehendes Bonebed in einer Mächtigkeit bis zu 20 cm. Die Sandsteine sind etwas über 6 m. mächtig entwickelt. Mit den Bonebed zusammen fand ich rhätische Muscheln. . . . Das Bonebed findet sich auch hier in mehreren Lagen übereinander, stellt nirgends einen durchgehenden Horizont dar und ist bald als rhätisches, bald als liasisches Bonebed anzusprechen." Koken (1908) has considered it probable that the types of *Tritylodon fraasi* and *Thomasia* were from the Liassic, and Ehrat finally concludes that probably the larger part of the bone-beds near the Rhaet-Lias border are to be considered as really Liassic. Schmierer (in Hennig, 1922) says, however, " Es handelte sich um das echte Grenzbonebed das an der Entnahmestelle mehrere zentimeter mächtig war, also nicht um die etwas höher in den Psilonotenschichten auftretende Schuppenbreccie." Which, if true, would apparently place the mammals in the Rhaetic. Hennig (1922) considers it highly probable that all the mammal teeth are of the same age, and he notes that a student, Daiber, found Liassic fossils in the bone-bed near Olgahain, which agrees with the general conclusion of Lörcher, Koken, Ehrat, and others, and would increase the probability that the mammals are of Liassic age.

An interesting new suggestion has, however, been made more recently by Hennig (1923). Fraas had supposed the bone-bed to be caused by the catastrophic flooding in of the Jurassic sea into the Triassic basin, but Hennig shows that the character of the bed disproves this. Most of the material consists of hard parts, very compact spines, scales, teeth, and so forth, and these are sorted according to weight and hardness. This, according to Hennig, would not be true of a primary deposit, nor would one expect to find such sudden changes from complete barrenness to great richness. He is led to the view that the bone-bed represents the residue of a thicker deposit with more complete fossils which was reworked before its consolidation, and he concludes that the bone-beds may be considered as containing Triassic fossils, even when the bed itself is in the Liassic.

This probably is not the final solution of the problem, for it can hardly be supposed that the bones and teeth are all as old as the oldest bone-beds, which range down into the true Keuper. The bones are obviously sorted and worn by the action of water, but this by no means necessarily suggests that they are derived from older deposits. There seems to be greater probability in the view that they represent a slow (but not secondary) accumulation in a shallow basin where sedimentation was proceeding slowly and where they were exposed to the action of the waves for some time before being buried.

From the very indefinite data available, the only conclusion which can now be drawn is that the German Mesozoic mammals are of uppermost Rhaetic or possibly even of Liassic age. They are apparently considerably younger than the English Triassic mammals, all of which occur well down in the Lower Rhaetic.

Stonesfield.

Fortunately, the geological conditions and exact horizon in which the Stonesfield mammals were found are well known, and do not leave the same room for doubt as in the case of the Rhaeto-Lias forms. The development of the Middle Jurassic in the Oxford district may be given as follows :

Middle Jurassic	Bathonian	Bradfordian	Cornbrash Forest Marble Stonesfield Slate
		Vesulian	Neaerean Beds Chipping Norton Lst. *Clypeus* Grit
	Bajocian	Bajocian *sens. strict.* Aalenian	Absent

Stratigraphic details regarding this region, and especially the Stonesfield slate, may be found particularly in Fitton, 1827, Woodward, 1894, and Pocock, Pringle *et al.* 1926. The " slate " is so called because of the use to which it has usually been put, as it actually varies from a rather limy sandstone to a gritty oolite and has no relationship to true slate. It is rather poorly exposed, and the larger part of our knowledge of it comes from examination of the quarries and mines in the vicinity of the village of Stonesfield. These are no longer worked and it is now difficult to obtain an adequate conception of the formation in the field. The following section by Fitton is the most enlightening one available :

Section of the Great Oolite at Stonesfield.

Upper Great Oolite.	Rubbly limestone	32′ 0″
	Clay with *Terebratula maxillata, Rhynchonella obsoleta, Pecten fibrosus*	
	" Rock " limestone	
	Blue clay	
	" Rock " oolite	
	Blue or greenish clay ; it effervesces slightly with acids and falls to pieces in water like fuller's earth	5′ 0″

Lower Great Oolite		"Rag" oolitic limestone, fine-grained, with casts of spiral univalves and bivalves, and coarse soft calcareous stone, more or less oolitic, forming the roof of the drift, or horizontal gallery, where the slate is dug..	25′ 0″
	Stonesfield Beds, 5′ 3″ to 6′ 0″.	"Soft-stuff," yellowish, very sandy clay including thin courses of fibrous gypsum	0′ 6″
		"Upper Head," composed of sand of varying composition and fineness of grain, containing towards the lower part large, spheroidal concretions (called "pot-lids"), of calcareous grit, pervaded by oolitic particles, these pot-lids furnish the best stone; the rock, with all the other useful stone of the pits, bears the common name of "Pendle." It includes pebbles of hard sparry oolitic stone	1′ 3″ to 1′ 6″
		"Manure" or "Race," slaty friable sand rock, calcareous to micaceous	1′ 0″
		"Cap" and "Lower Head"; the upper portion having a concretional form like that of the pot-lids. The rock in both cases varies from a very compact and fine-grained grit, effervescing strongly with acids, to a stone of which the larger portion consists of oolitic particles. The greater number of fossils, including Mammalian remains, *Trigonia impressa*, *Rhynchonella obsoleta*, etc., appear to have been derived from these beds..	1′ 6″ to 2′ 0″
		"Bottom-stuff"—coarser calcareous grit, with oolitic particles (base not seen)	1′ 0″

The known Stonesfield mammals occur in a light brown, very hard, calcareous sandstone, which splits readily into laminae—the typical "slate." In some, as BM 112, the rock is devoid of oolitic grains, while in others, as M 7595, these may be very frequent. There are numerous somewhat rusty casts of *Trigonia* on these slabs.

Like the Rhaetic deposits in which mammals occur, the Stonesfield is the deposit of a shallow sea and was laid down close to the shoreline. The fauna, while naturally entirely distinct from the Rhaetic systematically, is almost identical in facies. The life of the neighbouring land is represented by the mammals, two pterosaurs, *Megalosaurus*, insects, and plant remains, which last include a number of ferns, cycads, and conifers. Marine vertebrates include crocodiles, plesiosaurs, turtles, and numerous fishes, among which are sharks, ganoids, and a species of *Ceratodus*. The invertebrate fauna, like that of the Rhaetic, is dominated by the pelecypods, gastropods being less common and ammonites rare. Corals occur but are few in number.

Purbeck.

All the pertinent facts regarding the Purbeckian, especially as developed at the mammal locality, will be found in H. B. Woodward, 1895, and Strahan, 1898. The general section of the late Jurassic of the Isle of Purbeck is as follows:

Lower Cretaceous	Wealden
Upper Oolitic	Purbeck
	Portland
	Kimmeridge
Middle Oolitic	Corallian

The Wealden and Purbeck are entirely conformable and the Jurassic-Cretaceous boundary drawn between them is arbitrary, although, for many reasons not germane to the present discussion, it is the most useful one and is almost universally accepted. The Purbeck beds differ from those below them in being largely of brackish or freshwater origin and from those above them in being largely calcareous ; in neither case is any distinct time break manifest, although the contact with the Portland is unconformable, the transition from marine to freshwater conditions being abrupt. For present purposes the Durdlestone (or Durlston) section may be summarized as follows (based on Woodward, 1895) :

SECTION AT DURDLESTONE BAY.

WEALDEN.		
	Conformity } Not seen in Durdlestone cliffs.	
	Plaudina Clays }	
Upper Purbeck.	Upper *Cypris* Clays and Shales	45′ 10″
	Unio Beds	4′ 9″
	Upper Broken Shell Limestone	10′ 0″
		60′ 7″
Middle Purbeck.	Chief Beef Beds: Dark (alum) shales with "beef" and selenite, beds of limestone and layers of shells. *Cyrena* and Cyprides	29′ 11″
	Corbula Beds: Layers of shelly limestone, shale, alum shale, and marl, with "beef" and selenite. Turtle and fish remains (*Asteracanthus*), *Melanopsis harpaeformis*, *Cardium*, *Corbula alata*, *Cyrena*, *Modiola*, *Ostrea*, *Pecten*, *Perna*, *Thracia*. Insects and Cyprides	34′ 1″
	Scallop Beds: White (Roach) shelly limestones and occasional shale. Fish remains, *Corbula alata*, *Ostrea*, *Pecten*	4′ 6″
	Intermarine Beds: Upper building stones. More or less shelly limestones with shale partings. Saurian, turtle, and fish remains (*Hybodus*, *Lepidotus*), *Hydrobia*, *Limnaea*, *Melanopsis harpaeformis*, *Paludina*, *Cornula alata*, *Cyrena*, *Modiola*, *Ostrea*, *Serpula*, *Cypridea punctata*, plant remains..	46′ 0″
	Cinder Bed: Earthy limestone made up chiefly of *Ostrea distorta*, fish remains, *Cardium*, *Perna*, *Trigonia*, *Serpula*, *Hemicidaris purbeckensis*	8′ 6″
	Cherty and Marly Freshwater Beds:	
	Freshwater bed	10″
	"FEATHER." Insects, fishes, turtles, *Nuthetes destructor*, *Trioracodon major*	2′ 2″
	"CAP"—*Trioracodon ferox*	1′ 0″
	Shales and Limestones	6′ 6″
	"FLINT BED"—Marly limestone with black chert. Freshwater shells	3′ 0″
	Shale and marl..	2′ 8″
	Marl with thin limestone at top	1′ 2″
	Black shale, insect and fish remains..	1′ 0″
	Shales, marls, and limestones	10′ 3″
	Grey, earthy bed. All but two of the known mammal specimens	1′ 0″
		166′ 9″

Lower Purbeck.	Marly Freshwater Beds	7′ 4″
	Soft Cockle Beds	82′ 1″
	Hard Cockle Beds	10′ 0″
	Cypris Freestone	36′ 3″
	Broken Bands	15′ 0″
	Soft Cap	7′ 6″
	Hard Cap	11′ 0″
	Dirt Bed	0′ 3″
		169′ 5″
		396′ 9″

The mammals occur at three horizons in the lower part of the Middle Purbeck. The type, and only, specimen of *Trioracodon major* is from the Feather, about ten feet below the prominent and easily identified Cinder Bed. A maxilla of *Trioracodon ferox*, not the type, comes from the Cap, immediately below the Feather. All the other mammals come from the Dirt Bed which is at the base of the middle division of the Purbeck at this locality. It is most easily found by the fact that it is about fifteen feet below the readily recognizable Flint Bed, or about ten feet below the thin but distinctive black shale.

The exact spot from which the mammals of the Dirt Bed were derived is marked by an excavation known as Beckles' Cutting. This cutting was very much enlarged by the Willetts (*see* Willett, 1881), who scarped down the overlying strata to a depth of forty feet and exposed an area of the dirt bed measuring thirteen by ten feet. It is probable that the fine collection of Beckles represents the contents of an unusually fossiliferous pocket or lens, for the labours of the Willetts only yielded a single jaw. A Dirt Bed occurs at the same horizon at some other localities, as at Worbarrow Bay, but no mammals have so far been found in it elsewhere.

The conditions under which the Purbeck was laid down are not difficult to reconstruct. It is obviously the deposit chiefly of fresh waters on a flat low-lying region very close to the sea. The waters were marshy or lagoonal and were very sluggish, or indeed quite stagnant. The substratum consisted of the limestones of the Portland, and the Purbeck waters were saturated with lime, which not only furnished shell-building material for the abundant invertebrates, but was also deposited inorganically, as in the botryoidal limestones which occur at several horizons. Whether through actual fluctuations in relative level of land and sea, or through shifting of sandbars, or similar changes, the drainage conditions were liable to variation. Thus subaerial soils occur at several levels which mark the draining of the area, and in this soil were established forests of cycads and conifers. In some cases the stumps of these trees were deeply encased in tufa when the region was again flooded by the lime-saturated waters.

In the middle Purbeck the waters of the sea several times gained access to the area, although the facies is usually brackish rather than truly marine. The Upper Purbeck, again, is strictly non-marine and passes over into the Wealden. The latter is markedly different and denotes the influx into the region of a great river or rivers, heavily laden with sediment.

Invertebrates are abundant throughout, chiefly freshwater gasteropods and

pelecypods. Ostracods are common at some horizons, and insects (chiefly Coleoptera, Orthoptera, Neuroptera, Diptera, Hemiptera) are abundant locally. Of the vertebrates the inhabitants of the swampy waters, crocodiles, turtles, and ganoids are most common. A few fragments of dinosaurs (*Iguanodon, Echinodon*) occur, also a pterosaur and a rhynchocephalian, while the mammals and some presumable lacertilians may represent the arboreal life of the swamps. The marine element is seen in such molluscs as *Pecten, Thracia, Trigonia,* and *Avicula,* while a number of others are typical of brackish water. There is one echinid, *Hemicidaris,* also a few marine sharks, and Lydekker has recorded the isolated presence of a plesiosaur, but in general the groups typical of true open marine waters are absent—there are no ammonites, brachiopods, or corals.

Wealden.

All the known Wealden mammals are from the Hastings beds near Hastings, details of which are given in the Geological Survey Memoir of the Weald (Topley, 1875). The Lower Cretaceous section of the region is as follows:

- Lower Cretaceous
  - Upper Neocomian — Lower Greensand
  - Lower Neocomian — Wealden
    - Weald Clay
    - Hastings Beds
      - Tunbridge Wells Sand
      - Wahurst Clay
      - Ashdown Sands
      - Fairlight Clay

Five mammalian specimens are known. Three, representing *Loxaulax valdensis,* ? *Loxaulax* sp., and mammal indet., are from the Ashdown Sands, Fairlight Cliffs. One, mammal indet. ("*Plagiaulax dawsoni*" type), is from the Wadhurst Clay, Old Roar Quarry. The fifth, multituberculate indet. ("? *Bolodon* sp." of Lydekker), is stated to be from the Tilgate Grit, Hastings. The Tilgate Grit is not a definite stratum but is a hard calcareous sandstone occurring at irregular intervals throughout the Wadhurst Clay and, occasionally, in the Ashdown Sands. The specimen, moreover, is not in such a sandstone but in a very crumbly clay, so that its exact level must be considered very dubious. It was found many years before it was described and, apparently, was not in place when found. Indeed, it seems impossible to obtain an exact record of the horizon at which any specimen occurred. The Ashdown Sands are about 150 feet thick, the Wadhurst Clay over 100, but fortunately each is, so far as known, a paleontological unit. Under the circumstances the detailed section of these beds has no value for the present purpose, but their general characters may briefly be considered.

The Ashdown Sand is extremely varied. It consists predominately of grey, yellow, or white sandstone, sometimes indurated; of much clay, usually in beds thinner than the sandstone; and of lesser amounts of marl and some clay ironstone and lignite. *Loxaulax valdensis* and ? *Loxaulax* sp., which still remain in the matrix, are in a light coloured fine grit consisting of grains of quartz in a groundmass of

comminuted felspar, kaolin, and other minerals. Black teeth, scales, and bone fragments are scattered rather sparsely through the rock.

The Wadhurst Clay (like most fluviatile formations) is also extremely heterogeneous. It consists of alternations of clays, shales, and sandstones, but there are also beds of calcareous grit, of clay ironstone, and thin limestone layers, chiefly made up of *Cyrena* and *Paludina*. Fossils are abundant but not varied. There are some plant remains, chiefly fragments of lignite, ostracods, *Paludina*, *Cyrena*, and *Unio*. Vertebrate remains also occur, usually in a very fragmentary state in clayey strata, forming true bone beds in places. The genera represented are mainly *Hybodus*, *Lepidotus*, *Iguanodon*, also crocodiles and turtles. It was in such a bone-bed that the mammal tooth was found. Neither in this fauna, nor in the almost identical Ashdown one, are there any marine forms. *Hybodus* was, it is true, primarily marine, but it is obvious that it swam far up the great rivers of the time, as some sharks may do even to-day.

One interesting and important feature of the Purbeck and Wealden mammal discoveries, as opposed to those in the Rhaetic and Stonesfield, is that in the former deposits the mammal remains are apparently found not far from where they died and in strata which were deposited under much the same conditions as those which formed the living environment of the animals, that is, in low-lying, poorly drained, probably heavily forested or overgrown areas. The Rhaetic and Stonesfield deposits are marine and certainly represent conditions very different from those under which the mammals lived, although the other land animals, and the plant remains all point to the living conditions here, also, having been much the same as those of the Upper Jurassic and Lower Cretaceous mammals so far made known.

CORRELATION.

THE use of the Mesozoic Mammalia for the correlation of strata is naturally limited. They are few in number, and isolated in space and time. Nevertheless, in one case, that of the Purbeck and Morrison, they are the most important if not, indeed, the decisive, factor in correlation.

RHAETIC.

The only Rhaetic correlations possible by means of mammals are of little value. On quite different data it has been pointed out that the English forms are probably somewhat earlier than the German ones. The mammals neither definitely support nor contradict this view. No type is really common to the two faunas, if one may call them such, although the families are closely related.

Much the same may be said of the correlation of the German Rhaet-Lias with the Stormberg. The presence in Germany of a mammal, *Tritylodon fraasi*, which must be referred to a Stormberg genus, would seem to indicate approximate contemporaneity. The value of this observation is slight, however, when one recalls that the European specimen is lost and its identification depends on inadequate figures and descriptions, that its exact horizon and age are in question, and that the definite horizon and locality of the South African genus are quite unknown. The specimen on which the latter is based came from Basutoland, so far as known, and hence probably from the Stormberg Beds, which cover almost the entire area of that state; but Basutoland is large and the Stormberg represents a great duration of time. The age is uncertain. Broom has supposed it to be Liassic, but Haughton throws much doubt on the strongest of Broom's evidence and would place it, as formerly, in the Rhaetic. Both European and African forms are therefore either Rhaetic or Liassic —not a very useful conclusion.

UPPER JURASSIC.

The comparison between the much more complete Purbeck and Morrison faunas, on the other hand, is of great value and significance. Enough comparable genera are known to make a comparison of value, and the age of the Purbeck is not open to any doubt. Occurring at the top of a fine Jurassic series and itself containing representative marine fossils, it occupies a very definite place in the time-scale. The age of the Morrison, on the other hand, has been the subject of much controversy, and the definite light cast on this by the mammals is more than welcome.

A list of mammalian genera of the two formations, with identical genera united

by continuous lines and closely comparable ones by broken lines reveals a fairly close correspondence :

PURBECK.	MORRISON.
TRICONODONTA.	
Triconodon.	
Trioracodon. ———	*Trioracodon.*
	Priacodon.
	Aploconodon.
	Phascolodon.
SYMMETRODONTA.	
Peralestes. } - - - - - - - - - - - - - - -	*Tinodon.*
Spalacotherium. }	
	Amphidon.
MULTITUBERCULATA.	
Ctenacodon. ———	*Ctenacodon.*
Plagiaulax.	
Bolodon.	
	Psalodon.
PANTOTHERIA.	
Paurodontidae.	
Peramus.	
	Paurodon.
	Archeotrigon.
	Tathiodon.
Dryolestidae.	
Amblotherium. ———	*Amblotherium.*
Phascolestes. } - - - - - - - - - - - - - - -	{ *Dryolestes.*
Peraspalax. }	{ *Laolestes.*
Kurtodon.	
	Kepolestes.
	Herpetairus.
	Melandon.
	Malthacolestes.
	Miccylotyrans.
	Euthlastus.
	Pelicopsis.
Dicrocynodontidae.	
Peracynodon. - - - - - - - - - - - - - - - - -	*Dicrocynodon.*

Only one family, Amphidontidae, is not common to both, and it is so extremely rare in the Morrison that its apparent absence from the Purbeck is probably due only to non-discovery. Three genera, which happen to be among the most abundant and typical, and to belong to three different orders, are common to the two faunas—a sufficiently impressive fact when one recalls the great distance between them and the probably very limited migratory powers of these small beasts. At least as significant as this absolute correspondence, however, is the general agreement between the two faunas in constitution, which speaks for identity of environmental conditions, and in stage of development, which speaks for identity of age. There is much other evidence in favour of this view and it has been more fully discussed elsewhere (Simpson, 1926B).

Wealden.

Conclusions drawn from the evidence of the Wealden mammals must be entirely tentative, as only one tooth is known which can be positively identified. It can be said, however, that this one tooth is closely comparable to the Purbeck-Morrison plagiaulacids, but definitely more advanced than any known member of the latter group. This is in accord, so far as it goes, with the age relations of the Wealden and Purbeck, and with the view as to the age of the Morrison expressed above.

FAUNAL LISTS.

THE arrangement of this monograph, which is primarily zoological rather than geological, has often necessitated wide separation of the different elements of the same mammalian fauna. In order to place them in the appropriate geological units, and by way of review of the whole subject, the species recognized in the present revision are here gathered together into faunal lists. Only the European forms are included.

RHAETIC FAUNAS.

A. German Rhaeto-Lias :

Multituberculata
Tritylodontoidea
Tritylontidae
Tritylodon fraasi Lydekker
Oligokyphus triserialis Hennig
O. biserialis Hennig

? ? Plagiaulacoidea
Microcleptidae
Thomasia antiqua (Plieninger)

B. English Rhaetic

1. Watchet
? Multituberculata
? ? Plagiaulacoidea
? Microcleptidae
Hypsiprymnopsis rhaeticus Dawkins.

2. Holwell
? Multituberculata
? ? Plagiaulacoidea
Microcleptidae
Microcleptes mooreí (Owen)
M. fissurae Simpson
Thomasia anglica Simpson

These few species, with *Tritylodon longaevus*, are the only known Triassic mammals. *Dromatherium* and *Microconodon* from the Triassic of North Carolina

have long been considered as mammals, although with occasional protests, but a recent thorough re-study of the originals has convinced me of their reptilian nature.

The Triassic mammals, then, are all referred to the Multituberculata. Two genera, *Tritylodon* and *Oligokyphus*, belong to a distinct suborder otherwise known only from the Middle Jurassic—a suborder so distinctive that it can hardly be supposed to have entered into the history of those later and more typical multituberculates, the Plagiaulacoidea, at all. This group, which, thanks to the skull from South Africa, must be considered as fairly well known, is an early Mesozoic one with no particular bearing on the phylogeny of later mammals.

The other Triassic mammals are placed in the genera *Thomasia*, *Hypsiprymnopsis*, and *Microcleptes*, all represented only by isolated teeth. These teeth are very peculiar; there is not enough resemblance to anything else to enable one to place them definitely. If they belong to any Mesozoic order otherwise known it must be to the Multituberculata, and it is possible, although not especially probable, that they represent an early offshoot of the plagiaulacoid stock.

Many writers have spoken of the appearance of definite mammalian forerunners in the Triassic, and of the inevitable conclusion that mammals must have originated in the Permian. They may have done so, but the evidence is a scientific myth. Mammals of a sort do appear at the very top of the Triassic (though some would even place them in the lowest Jurassic), separated by the whole of a long geological period from the Permian. But these mammals have no certain relationship even to the later multituberculates, and as for any relationship with Tertiary or recent mammals or their ancestors, it is hardly incautious to say that this is quite impossible. The earliest mammals which can be considered as related to this ancestry appear in the Middle Jurassic. Their time of origin is not necessarily related to that of the known Triassic "mammals." They may have arisen in the Permian, although this is improbable and leaves a long and unnecessary blank space, besides ignoring the fact that the cynodonts were advancing steadily towards a mammalian structure throughout the Triassic. It is very probable that they may have originated in the Triassic, even well along in this period. It is possible, but improbable, that they originated in the Lower Jurassic. At present, at any rate, much more may be learned about mammalian history in the Triassic from the cynodont reptiles than from the known Triassic mammals.

STONESFIELD FAUNA.

Multituberculata
- Tritylodontoidea
  - Tritylodontidae
    - *Stereognathus ooliticus* Charlesworth.

Triconodonta
- Triconodontidae
  - Amphilestinae
    - *Amphilestes broderipii* Owen
    - *Phascolotherium bucklandi* (Broderip)

Pantotheria
Amphitheriidae
Amphitherium prevostii (H. v. Meyer)

This is the only known Middle Jurassic fauna and it is the earliest known mammalian assemblage which can be supposed to have much significance for mammalian history as a whole. One element in it, *Stereognathus*, appears to be a last survivor of a group already found in the Rhaetic. The others as true mammals appear for the first time. *Amphitherium* is probably the most significant single genus of Mammalia known, for it represents a very early, very generalized stock, which, so far as known, provides an ideal structural ancestor for all known post-Paleocene mammals, except monotremes.

PURBECK FAUNA.

Multituberculata
Plagiaulacoidea
Plagiaulacidae
Plagiaulax becklesii Falconer
Ctenacodon minor (Falconer)
C. falconeri (Owen)
Bolodon crassidens Owen
B. osborni Simpson
B. elongatus Simpson
Triconodonta
Triconodontidae
Triconodontinae
Triconodon mordax Owen
Trioracodon ferox (Owen)
T. oweni Simpson
T. major (Owen)
Symmetrodonta
Spalacotheriidae
Spalacotherium tricuspidens Owen
Peralestes longirostris Owen
Pantotheria
Paurodontidae
Peramus tenuirostris Owen
Dicrocynodontidae
Peraiocynodon inexpectatus Simpson
Dryolestidae
Amblotherium pusillum (Owen)
Amblotherium nanum (Owen)
Kurtodon pusillus Osborn
Peraspalax talpoides Owen
Phascolestes mustelula (Owen)

The Purbeck mammalian fauna and the Morrison fauna, which resembles it very closely, present four distinct major divisions. The first are the plagiaulacoid multituberculates, which here appear for the first time (unless, indeed, the microcleptids are related to this stock) but which must have been in existence since the Triassic. They endured for a long time after this, however, for they continued

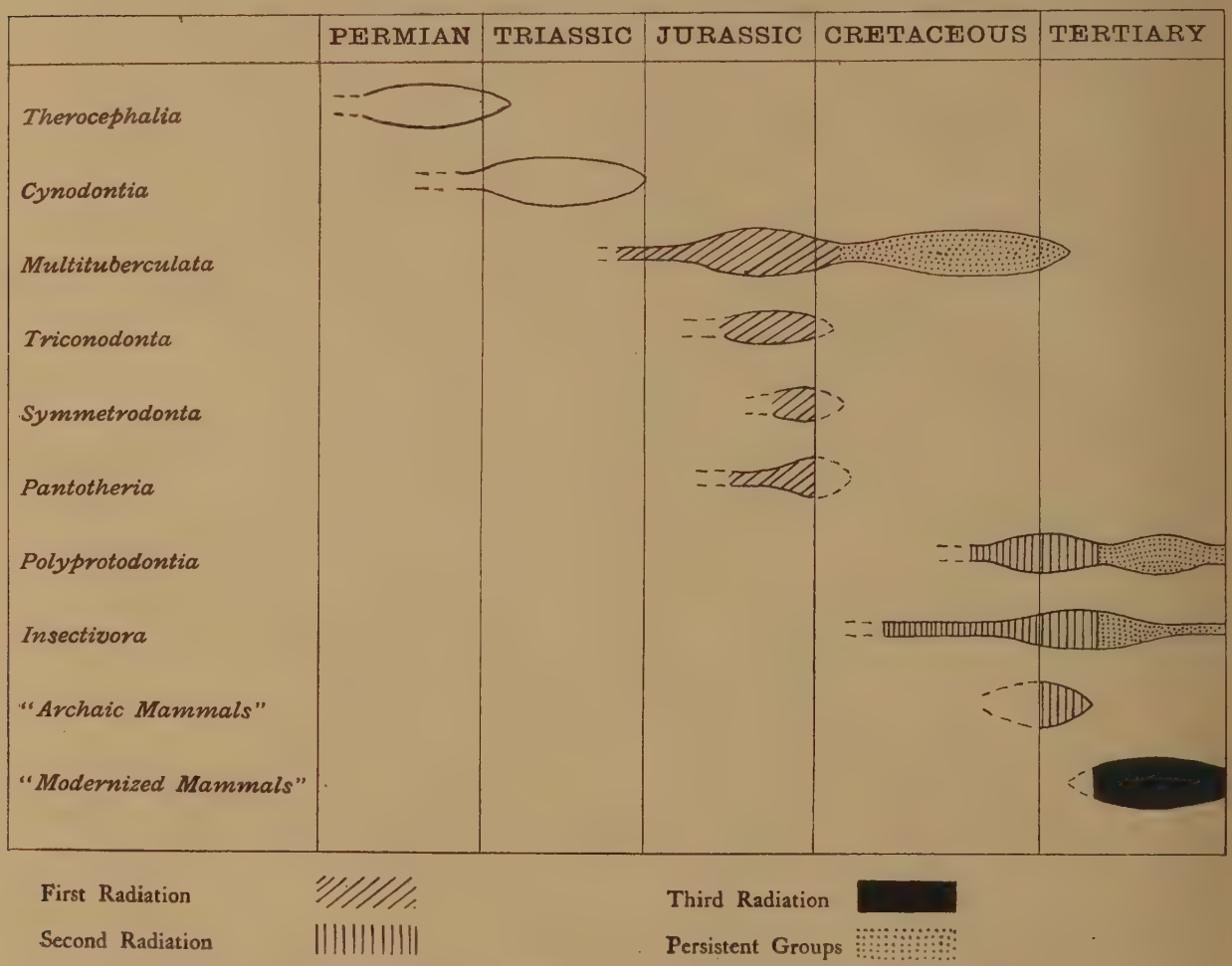


FIG. 56.—Diagram of the geological distribution of the mammals and their immediate ancestors.

through the Cretaceous and the Paleocene and into the base of the Eocene before vanishing without issue.

The triconodonts here make their last appearance. They differ but little from the Middle Jurassic forms.

The symmetrodonts are known only from these two formations (Purbeck and Morrison). They seem to represent a very early and distinctive offshoot from the

pantotherian or pre-pantotherian stock. Like the triconodonts they do not appear again, and like them also the group leaves no recognizable descendants.

It is the pantotheres that are most abundant, varied, and interesting. Although still very primitive and readily derivable from *Amphitherium*, they have lost almost entirely the generalized nature of that genus. The main mammalian stem is not here; these are marginal, probably swamp-dwelling groups. They represent the main stock, however, in a structural way; and by taking the characters common to all, ignoring their peculiar little specializations, an adequate idea of the stage of evolution reached by the ancestral Theria in the Upper Jurassic is believed to be obtainable. The paurodontids have departed least from the central stock, but they are swinging towards an extreme reduction in cheek-tooth number, probably accompanied by changes in the jaw and even tooth degeneration. The dicrocynodonts have become superficially specialized in a rather amazing and very aberrant way. The dryolestids are specializing in quite another manner, although their departure from the amphitheriid ancestor is not extreme.

Wealden Fauna.

Multituberculata
Plagiaulacoidea
Plagiaulacidae
Loxaulax valdensis (Smith Woodward)

Several teeth are known from the Wealden, but of these only one is really identifiable. All appear to be plagiaulacoids, and the best preserved one is clearly a plagiaulacid which is more advanced than any known Purbeck-Morrison form, but much closer to them than to the Upper Cretaceous and Paleocene ptilodontids.

There is no direct evidence as to the real character of the Cretaceous mammal faunas of Europe. The Upper Jurassic fauna, and that of the Paleocene (Cernaysian) are very much like the corresponding ones of North America in composition, and there may, therefore, be some reason to suppose that the Cretaceous faunas were so too. The known American Upper Cretaceous mammal faunas consist of multituberculates (ptilodontids) in great number and variety, didelphids, also varied and numerous, and a few rare insectivores. It has been suggested that this was a facies only of the American fauna of the time and that elsewhere there may have been faunas which would contain a larger placental element. At present this can neither be proved nor disproved, but multituberculate-marsupial faunas were certainly very widespread and it is a fauna of this kind which one would expect, *a priori*, to find in Europe also at that time. It is in the Upper Cretaceous that marsupials make their first appearance as such—a statement which cannot be too strongly emphasized in view of the universal tendency to refer any and all of the Mesozoic mammals to the Marsupialia. The earliest definitely differentiated insectivores also appear in the Cretaceous.

The mammalian fauna of the Paleocene, while archaic and representing a probable modifed survival of an unknown Cretaceous assemblage, contains few elements

which really recall the Mesozoic mammals as they are known. In the Cernaysian, oldest of European Tertiary faunas, ptilodontids are still present and not greatly advanced over the Upper Cretaceous types, but it is their last appearance. Only a single very rare didelphid occurs, while the insectivores are not especially suggestive of those known from the Mesozoic, and a number of other groups appear for the first time. The ordinal differentiation of mammals has already occurred.

LIST OF WORKS CONSULTED

THE following list is believed to contain references to all original contributions to our knowledge of the Mesozoic Mammalia of Europe. In addition to this, only such works are listed as are specifically cited in the text. No attempt has been made to refer to the almost innumerable works which mention the Mesozoic mammals incidentally, but which contain nothing to add to, or alter, the current knowledge or conception of them.

ABEL, OTHENIO. 1919. Die Stämme der Wirbeltiere, pp. xviii+914, 8vo. Berlin u. Leipzig.

——. 1923. Ueber einen Multitberkulaten a. d. Miozän d. Nordpazifischen Küsten Region. *Paläont. Zeitsch.*, V, pp. 213–225.

AGASSIZ, JEAN LOUIS RODOLPHE. 1838. *See* BUCKLAND, W., 1838.

——. 1835. [No title.] *N. Jahrb. Min. Geol. Paläont.*, pp. 185–186.

AMEGHINO, FLORENTINO. 1891. Los plagiaulacideos argentinos y sus relaciones, etc. *Rev. Argent. Hist. Nat.*, I, pp. 38–44.

——. 1903. Los diprotodontes del orden de los plagiaulacoideos. *An. Mus. Nac. Buenos Aires*, IX.

BENSLEY, BENJAMIN ARTHUR. 1902. On the Identification of the Meckelian and Mylohyoid Grooves in the Jaws of Mesozoic and Recent Mammals. *Univ. Toronto Studies (Biol.)*, III, pp. 75–81, one pl.

BLAINVILLE, HENRI MARIE DUCROTAY DE. 1838A. Doutes sur le prétendu Didelphe de Stonesfield. *C. R. Acad. Sci. Paris.*, VII, pp. 402–418.

——. 1838B. Nouveaux doutes, etc. *Idem.*, VII, pp. 727–736.

BRANCA, W. 1915. Einige Betrachtungen ü. d. ältesten Säuger d. Trias- u. Lias-zeit. *Abh. pr. Akad. Berlin*, 1915, No. 5, pp. 1–77.

BRODERIP, WILLIAM JOHN. 1828. Observations on the Jaw of a Fossil Mammiferous Animal found in the Stonesfield Slate. *Zool. Journ. London*, III, pp. 408–412, pl. xi.

BROOM, ROBERT. 1905A. On the Affinities of Tritylodon. *Trans. S. African Phil. Soc.*, XVI, pp. 73–77.

——. 1905B. On Some Points in the Anatomy of the Theriodont Reptile Diademodon. *Proc. Zool. Soc. London*, 1905, pp. 96–102, pl. x.

——. 1907. On the Origin of Mammals. *Rep. Brit. Ass.*, III, pp. 437–438.

——. 1910. On Tritylodon and on the Relationships of the Multituberculata. *Proc. Zool. Soc. London*, 1910, pp. 760–768.

——. 1914. On the Structure and Affinities of the Multituberculata. *Bull. Am. Mus. N. H.*, XXXIII, pp. 115–134, pls. xi, xii.

BUCKLAND, WILLIAM. 1824. Notice on Megalosaurus. *Trans. Geol. Soc. London*, (2), I, pp. 390–396, pls. xl–xliv.

——. 1836. Geology and Mineralogy, considered with reference to Natural Theology. Bridgewater Treatises, VI. I, pp. xvi+600 ; II, vii+128, pls. i–lxix, 8vo, London.

——. 1838–1839. Geologie und Mineralogie in Beziehung zur Natürlichen Theologie. 1839, I, xii+666 ; 1838, II, Tafeln i–lxix u Erklarung ; 8vo, Neufchatel.

Translated and annotated by L. Agassiz. Vol. II, Plates. (Vol. I was published in 1839, the date usually erroneously given for Vol. II also.)

CARTER, J. THORNTON. 1922. On the Structure of the Enamel in the Primates and some other Mammals. *Proc. Zool. Soc. London*, 1922, pp. 599–608, pls. i–vii.

[CHARLESWORTH, EDWARD.] 1838. [Unsigned note.] *Athenaeum*, 6 October, 1838.

——. 1855. [No title.] *Rep. Brit. Ass.* 1854 (Liverpool), Abstracts, p. 80.

COPE, EDWARD DRINKER. 1884. The Tertiary Marsupialia. *Amer. Nat.*, XVIII, pp. 686–697.

——. 1887. The Marsupial Genus Chirox. *Amer. Nat.*, XXI, pp. 566–567.

——. 1888. The Multituberculata Monotremes. *Amer. Nat.*, XXII, p. 259.

CUVIER, GEORGES LEOPOLD CHRÉTIEN FRÉDÉRIC DAGOBERT. 1825. Récherches sur les Ossemens Fossiles de Quadrupèdes, 3rd ed., V, pp. 1–547, pls. i–xxxiii, 4to, Paris.

DAWKINS, WILLIAM BOYD. 1864. On the Rhaetic Beds and White Lias of Western and Central Somerset, and on the Discovery of a New Fossil Mammal in the Grey Marlstones beneath the Bone-bed. *Quart. J. Geol. Soc. London*, XX, 396–412.

DEWOLETZKY, RUDOLF. 1898. Offene Fragen aus d. Gesch. d. niederen Säuger. *Jahr. Ber. Nieder-Oest. Land.-Realgymn. Mödling*, 1898.

DÖDERLEIN, LUDWIG. 1921. Betrachtungen über d. Entwick. d. Nahrungsaufnahme bei Wirbeltieren. *Zoologica*, XXVII, Heft 71, pp. 1–59.

DUMÉRIL, ANDRÉ MARIE CONSTANT. 1838. Rémarque . . . à l'occasion du Mémoire de M. de Blainville. *C. R. Acad. Sci. Paris*, VII, p. 736.

EARLE, CHARLES. *See* OSBORN, H. F., & EARLE, C.

EHRAT, HANS. 1920. Die Rhätformation und Rhät-Liasgrenze in Schwaben. Inaug.-Diss. pp. 84, 8vo, Tübingen.

ENDLICH. 1870. Das Bonebed Württemebergs. Inaug.-Diss. Tübingen.

FALCONER, HUGH. 1857. Description of Two Species of the Fossil Mammalian Genus Plagiaulax from Purbeck. *Quart. J. Geol. Soc. London*, XIII, pp. 261–282.

——. 1862. On the Disputed Affinity of the Mammalian Genus Plagiaulax. *Quart. J. Geol. Soc. London*, XVIII, pp. 348–369.

FITTON, WILLIAM HENRY. 1828. On the Strata whence the Fossil described in the Preceding Notice [Broderip, 1828] was obtained. *Zool. Journ.*, III, pp. 412–418.

FLOWER, WILLIAM HENRY. 1883. Mammalia. *Encyclopaedia Britannica*, 9th ed., XV.

FLOWER, WILLIAM HENRY, & LYDEKKER, RICHARD. 1891. An Introduction to the Study of Mammals Living and Extinct. pp. xvi+763, 8vo, London.

FRAAS, OSCAR FRIEDRICH VON. 1866. Vor der Sündflut. Stuttgart.

GIDLEY, JAMES WILLIAM. 1909. Notes on the Fossil Mammalian Genus Ptilodus with Descriptions of New Species. *Proc. U.S. Nat. Mus.*, XXXVI, pp. 611–626.

GILL, THEODORE NICHOLAS. 1872. Arrangement of the Families of Mammals, etc. *Smithsonian Misc. Coll.*, No. 230.

GOODRICH, EDWIN STEPHEN. 1894. On the Fossil Mammalia of the Stonesfield Slate. *Quart. J. Micr. Sci.*, XXXV, pp. 407–431, pl. xxvi.

GORE, JOHN ELLARD. 1874. Glossary Fossil Mammals. pp. 51, 8vo, Roorkee.

GRANGER, WALTER. 1915. New Evidence of the affinities of the Multituberculata. (Abstract.) *Bull. Geol. Soc. Amer.*, XXVI, p. 152.

GRANT, ROBERT EDMUND. 1838. In "*Thompson's British Annual*" for 1839.

GREGORY, WILLIAM KING. 1910. The Orders of Mammals. *Bull. Amer. Mus. N. H.*, XXVII, pts. 1, 2.

——. 1922. The Origin and Evolution of the Human Dentition. pp. xviii+548, 8vo, Baltimore.

HAECKEL, ERNST. 1895. Systematische Phylogenie d. Wirbeltiere, etc. pp. xx+660, 8vo, Berlin.

HENNIG, EDWIN. 1922. Die Säugerzähne des württembergischen, Rhät-Lias-Bonebeds. *N. Jahrb. Min., Geol., Paläont.*, Beil. Bd., XLVI, pp. 181–267, pls. ii–v.

——. 1923. Geologie von Württemberg nebst Hohenzollern. pp. vi+383, pls. i–ix, 8vo, Berlin.

——. 1927. Die Pioniere des Säugetier-Stammes. *Natur und Museum*, V, pp. 201–209.

HERTZ, MATHILDE. 1925. Beobachtungen an primitiven Saugetiergebissen. *Ztschr. wiss. Biologie*, Abt. A, IV (id. ac. *Ztschr. Morphol. Oekol.*), pp. 540–576, pl. xiii.

HINTON, MARTIN ALISTAIR CAMPBELL. 1926. Monograph of the Voles and Lemmings. Vol. I. Brit. Mus. (N. H.), pp. xvi+488, 15 plates, 8vo, London.

HUENE, FRIEDRICH VON. 1925A. Triassische Säugetierzahn aus Südwest-afrika. *ZentBl. Min. Geol. Paläont.*, Abt. B, pp. 174–181.

——. 1925B. Berichtigung: *Archaeodon* statt *Archaeotherium*. *Idem.*, Abt. B, p. 303.

HUXLEY, THOMAS HENRY. 1880. Application of the Laws of Evolution to the Arrangement of the Vertebrata and more particularly of the Mammalia. *Proc. Zool. Soc. London*, 1880, pp. 649–661.

JAEGER, GEORG FRIEDRICH VON. 1850. Uebersicht d. fossilen Säugetiere Württembergs. *Nov. Act. Acad. Caesar Leop. Nat. Cur.*, XV, ii, pp. 765–933, pls. lxviii–lxxii.

KRAUSSE, ANTON HERMANN. 1919. Hexapodologische Notizen. No. 53. *Arch. Naturg.*, LXXXIII, (A) (6), pp. 49–55.

LANKESTER, EDWIN RAY. 1861. [Letter signed "E. Ray."] *Geologist*, IV, p. 310.

LÖRCHER, O. Beiträge zur Kenntniss des Rhäts in Schwaben. Diss. Tübingen.

LYDEKKER, RICHARD. 1887. Catalogue of the Fossil Mammalia in the British Museum, V, pp. xxxv +345, 8vo, London.

——. 1893. On a Mammalian Incisor from the Wealden of Hastings. *Quart. J. Geol. Soc.*, XLIX, pp. 281–283.

——. 1894. Life and Rock, pp. xi+221, 8vo. London. [Chap. XII—The Oldest Mammals.]

——. 1896. A Geographic History of Mammals. pp. xii+400, 8vo. London.

——. *See also* FLOWER, W. H., & LYDEKKER, R.

——. *See also* NICHOLSON, H. A., & LYDEKKER, R.

LYELL, CHARLES. 1855. Manual of Elementary Geology. Ed. 5, pp. xvi+655, 8vo. London.

MAJOR, CHARLES IMMANUEL FORSYTH. On some Miocene Squirrels. *Proc. Zool. Soc. London*, 1893, pp. 179–215, pls. viii–xi.

MARSH, OTHNIEL CHARLES. 1880. Notice of New Jurassic Mammals representing Two New Orders. *Am. Jour. Sci.*, (3), XX, pp. 235–239.

——. 1885. On American Jurassic Mammals. *Rept. Brit. Ass., Montreal*, pp. 734–736.

——. 1887. American Jurassic Mammals. *Am. Jour. Sci.*, (3), XXXIII, pp. 327–348, pls. vii–x.

——. 1896. The Age of the Wealden. *Am. Jour. Sci.*, (4), I, p. 234.

MATTHEW, WILLIAM DILLER. 1916. A Marsupial of the Belly River Cretaceous. *Bull. Am. Mus. N. H.*, XXXV, 477–500.

——. 1922. [Notes in GEGRORY, 1922.]

MEYER, HERMAN VON. 1832. Palaeologica. pp. xi+560, 8vo. Frankfurt a/M.

MOORE, CHARLES. 1867. On the Abnormal Condition of Secondary Deposits. *Quart. J. Geol. Soc. London*, XXIII, pp. 449–568, pls. xiv–xvii.

NEUMAYR, MELCHIOR. 1884. Triglyphus und Tritylodon. *N. Jahrb. Min. Geol. Paläont.*, 1884, pp. 279–280.

NICHOLSON, HENRY ALLEYNE, & LYDEKKER, RICHARD. 1889. A Manual of Paleontology, 3rd ed., Vol. II. London.

OGILBY, WILLIAM. 1838. Observations on the Structure and Relations of the Presumed Marsupial Remains from the Stonesfield Oolite. *Proc. Geol. Soc. London*, III, pp. 21–23.

OSBORN, HENRY FAIRFIELD. 1887A. On the Structure and Classification of the Mesozoic Mammalia. *Proc. Acad. Nat. Sci. Philadelphia*, 1887, pp. 282–292.

——. 1887B. A Pineal Eye in the Mesozoic Mammals. *Science*, (2), IX, p. 92.

——. 1887C. The Pineal Eye in Tritylodon. *Science*, (2), IX, p. 114.

OSBORN, HENRY FAIRFIELD. 1887D. No Parietal Foramen in Tritylodon. *Science*, (2), IX, pp. 538.

——. 1887E. The Origin of the Tritubercular Type of Mammalian Dentition. *Science*, (2), X, p. 300.

——. 1888A. On the Structure and Classification of the Mesozoic Mammalia. *Journ. Acad., Nat. Sc. Philadelphia*, IX, pp. 186–264, pls. viii–ix.

——. 1888B. Additional Observations upon the Structure and Classification of the Mesozoic Mammalia. *Proc. Acad. Nat. Sc. Philadelphia*, 1888, pp. 292–301.

——. 1888C. The Mylohyoid Groove in the Mesozoic and Recent Mammalia. *Amer. Nat.*, XXII, pp. 75–76.

——. 1888D. The Evolution of the Mammalian Dentition to and from the Tritubercular Type. *Idem.*, XXII, pp. 1067–1079, pls. xxv–xxvi.

——. 1888E. A Review of Mr. Lydekker's Arrangement of the Mesozoic Mammalia. *Idem.*, XXII, pp. 232–236.

——. 1893A. Fossil Mammals of the Upper Cretaceous. *Bull. Am. Mus. N. H.*, V, pp. 311–330, pls. vii–viii.

——. 1893B. The Rise of the Mammalia in North America. *Amer. Jour. Sci.*, (3), XLVI, pp. 379–392, 448–466, pl. xi.

——. 1907. Evolution of Mammalian Molar Teeth. pp. ix+250, 8vo. New York & London.

OSBORN, H. F., & EARLE, C. 1895. Fossil Mammals of the Puerco Beds. *Bull. Am. Mus. N. H.*, VII, pp. 1–70.

OWEN, RICHARD. 1838A. On the Jaws of the *Thylacotherium prevostii* (Valenciennes) from Stonesfield. *Proc. Geol. Soc. London*, III, pp. 5–9.

——. 1838B. Description of the Remains of Marsupial Mammalia from the Stonesfield Slate. *Proc. Geol. Soc. London*, III, pp. 17–21.

——. 1842. Observations on the Fossils Representing the *Thylacotherium prevostii* (Valenciennes), etc. *Trans. Geol. Soc. London*, (2), VI, pp. 47–65.

——. [1844]–1846. History of British Fossil Mammals and Birds. pp. xlvi+560, 8vo. London.

——. 1854. On some Fossil Reptilian and Mammalian Remains from the Purbecks. *Quart. J. Geol. Soc. London*, X, pp. 420–433.

——. 1857. On the Affinities of *Stereognathus Ooliticus*, etc. *Quart. J. Geol. Soc. London*, XIII, pp. 1–11, pl. i.

——. 1859. Paleontology, in Encyclopaedia Brit., XVII.

——. 1860. Paleontology, or a Systematic Summary of Extinct Animals and their Geological Remains, pp. xv+420, 1 pl., 8vo, Edinburgh.

——. 1866. Description of Part of the Lower Jaw of a Small Oolitic Mammal, etc. *Geol. Mag. London*, (1), III, pp. 199–201, pl. x.

——. 1868. On the Anatomy of Vertebrates, III, Mammals, 8vo, London.

——. 1871. Monograph of the Fossil Mammalia of the Mesozoic Formations. *Paleontogr. Soc.*, XXIV.

——. 1877. Researches on the Fossil Remains of the Extinct Mammals of Australia with a Notice of the Extinct Marsupials of England, I, pp. xv+522; II, pp. 9, pls. i-cxxxi; 4to, London.
[Pages 1–104 and plates i–iv are exactly reprinted from the same pages and plates of Owen, 1871.]

——. 1884. On the Skull and Dentition of a Triassic Mammal (*Tritylodon longaevus*) from South Africa. *Quart. J. Geol. Soc. London*, XL, pp. 146–152, pl. vi.

——. 1885. Note on the Resemblance of the Upper Molar Teeth of an Eocene Mammal (*Neoplagiaulax* Lemoine) to those of Tritylodon. *Quart. J. Geol. Soc. London*, XLI, pp. 28–29.

PETRONIEVICS, BRANISLAUS. 1917. On the Skull of *Tritylodon longaevus*, Owen. *Ann. Mag. Nat. Hist.*, (8), XX, pp. 283–289, pl. x.

——. 1918. Note on the Lower Jaw of *Stereognathus ooliticus* Charlesworth. *Ann. Mag. Nat. Hist.*, (9), I, pp. 67–69, pl. iii.

——. 1922. Note on Root Division in the Molar Teeth of *Tritylodon*. *Ann. Mag. Nat. Hist.*, (9), X, pp. 216–217.

PHILLIPS, JOHN. 1871. The Geology of Oxford and the Valley of the Thames. pp. xxiv+523, pls. i-xv, 2 maps, 8vo, Oxford.

PLIENINGER, WILHELM HEINRICH THEODOR VON. 1847. Zähne aus der oberen Grenzbreccie des Keupers bei Degerloch und Steinenbronn. *Jahresh. Ver. Naturk. Württ.*, 1847, pp. 164–167.

POCOCK, PRINGLE, *et Al.* 1926. Geology of the Country around Oxford. 2nd. ed., *Mem. Geol. Survey*, 8vo, London.

POCHE, FRANZ. 1904. Richtigstellung einiger Gattungsnamen unter den Säugern. *Zool. Annalen*, I, pp. 47–49.

——. 1908. Einige notwendige Änderungen in der mammalogischen Nomenclatur. *Zool. Annalen*, II, pp. 269–272.

PRÉVOST, LOUIS CONSTANT. 1825. Observations sur les schistes calcaires oolitiques de Stonesfield en Angleterre. *Ann. Sci. Paris*, IV, pp. 389–416.

RICHARDSON, L. 1911. The Rhaetic and Contiguous Deposits of West, Mid, and part of East Somerset. *Quart. Journ. Geol. Soc.*, LXXII, pp. 1–74, pls. i–iv.

ROMER, ALFRED SHERWOOD. 1922. The Locomotor Apparatus of Certain Primitive and Mammal-like Reptiles. *Bul. Am. Mus. N. H.*, XLVI, pp. 517–606.

——. 1924. The Lesser Trochanter of the Mammalian Femur. *Anat. Record*, XXVIII, pp. 95–102.

SEELEY, HARRY GOVIER. 1879. Note on a Femur and a Humerus of a Small Mammal from the Stonesfield Slate. *Quart. J. Geol. Soc. London*, XXXV, pp. 456–463.

——. 1888. On the Nature and Limits of Reptilian Characters in Mammalian Teeth. *Proc. Roy. Soc.*, XLIV, pp. 129–141.

——. 1893. On a Reptilian Tooth with Two Roots. *Ann. Mag. Bat. Hist.*, (6), XII, pp. 227–30, 274–276.

——. 1895. Researches on . . . the Fossil Reptilia. Part IX, Sect. 2. The Reputed Mammals of the Karro Formation. *Phil. Trans. R. S. London*, (B), CLXXXVI.

SHERBORN, CHARLES DAVIES. *See* WOODWARD, A. S., & SHERBORN, C. D.

SIMPSON, GEORGE GAYLORD. 1925A. Mesozoic Mammalia, I. American Triconodonts. *Am. Jour. Sci.*, (5), X, pp. 145–165, 334–358.

——. 1925B. Mesozoic Mammalia, II. Tinodon and its Allies. *Am. Jour. Sci.*, (5), X, pp. 451–470.

——. 1925C. A Mesozoic Mammal Skull from Mongolia. *Am. Mus. Novitates*, No. 201.

——. 1925D. Mesozoic Mammalia, III. Preliminary Comparison of Mesozoic Mammals except Multituberculates. *Am. Jour. Sci.*, (5), X, pp. 559–569.

——. 1926A. Mesozoic Mammalia, IV. The Multituberculates as Living Animals. *Am. Journ. Sci.*, (5), XI, pp. 228–250.

——. 1926B. The Fauna of Quarry Nine. *Am. Journ. Sci.*, (5), XII, pp. 1–16.

——. 1926C. The Age of the Morrison. *Am. Journ. Sci.*, (5), XII, pp. 198–216.

STRAHAN, AUBREY. 1898. Geology of the Isle of Purbeck and Weymouth. *Mem. Geol. Survey*, 8vo, London.

THOMAS, OLDFIELD. 1887. On the Homologies and Succession of the Teeth in the Dasyuridae, etc. *Phil. Trans. R. S. London*, CLXXVIII.

TOPLEY, WILLIAM. 1875. Geology of the Weald. *Mem. Geol. Survey*, 8vo, London.

VALENCIENNES, ACHILLE. 1838. Observations sur les mâchoires fossiles des couches oolithiques de Stonesfield. *C. R. Acad. Sci. Paris*, 1838, VII, pp. 572–580.

WILLETT, EDGAR W., & WILLETT, HENRY. 1881. Notes on a Mammalian Jaw from the Purbeck Beds at Swanage, Dorset. *Quart. J. Geol. Soc. London*, XXXVII, pp. 376–380.

WILLETT, H. *See* WILLETT, E. W., & WILLETT, H.

WINGE, HERLUF. 1893. Jordfundne og nulevende Pungdyr (Marsupialia) fra Lagoa Santa. Minas Geraes, Brasilien. *E Museo Lundii*, II, pp. 149, pls. i-iv, 40. Copenhagen.

——. 1923. Pattedyr-Slaegter. Vol. I. pp. vii+360, pls. i–iii, 8vo. Copenhagen.

W[INWOOD], HENRY HOYTE. 1888. Handbook to the Geological Museum. pp. 15, 8vo. Bath.

WEBER, MAX. 1904. Die Säugetiere. pp. xi+866, 8vo. Jena.

WOODWARD, ARTHUR SMITH. 1891. On a Mammalian Tooth from the Wealden Formation of Hastings. *Proc. Zool. Soc. London*, pp. 585–586.

——. 1898. Outlines of Vertebrate Paleontology. pp. xxiv+470, 8vo. Cambridge.

——. 1911. On some Mammalian Teeth of the Wealden of Hastings. *Quart. J. Geol. Soc. London*, LXVII. pp. 278–281.

——. 1912. Notes on a Maxilla of *Triconodon* from the Middle Purbeck Beds of Swanage. *Proc. Geol. Ass. London*, XXIII, pp. 100–101, pl. xv.

——. 1916. On a Mammalian Mandible (*Cimolestes cutleri*) from an Upper Cretaceous Formation in Alberta, Canada. *Proc. Zool. Soc. London*, pp. 525–528.

——. *See also* WOODWARD, A. S., & SHERBORN, C. D.

WOODWARD, ARTHUR SMITH, & SHERBORN, CHARLES DAVIES. 1890. A Catalogue of British Fossil Vertebrata. pp. xxxv+396, 8vo, London.

WOODWARD, HENRY BOLINGBROKE. 1894. The Lower Oolitic Rocks of England. *Mem. Geol. Survey*, 8vo, London.

——. 1895. The Middle and Upper Oolitic Rocks of England. *Mem. Geol. Survey*, 8vo, London.

ZITTEL, KARL ALFRED VON. 1893. Handbuch der Palaeontologie. I Abt. IV Bd. Munich & Leipzig.

ZITTEL, KARL ALFRED VON, BROILI, FERDINAND, and SCHLOSSER, MAX. 1923. Grundzüge der Paläontologie. II. 4e Aufl. pp. v+706, 8vo. Munich & Berlin.

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PLATE I.

PAGE

Tritylodon longaevus Owen 11

Upper Triassic, Thaba N'chou, Basutoland.

FIG. 1.—Anterior part of skull from above. Natural size. HOLOTYPE. Brit. Mus. M 1951.

FIG. 2.—Same, viewed from below.

FIG. 3.—Same, viewed from left side.

Microcleptes moorei (Owen) 56

Rhaetic, Holwell, Somerset.

FIG. 4.—Crown view of cheek-tooth : stereoscopic. × 20 diam. Yale Peabody Museum 13622A.

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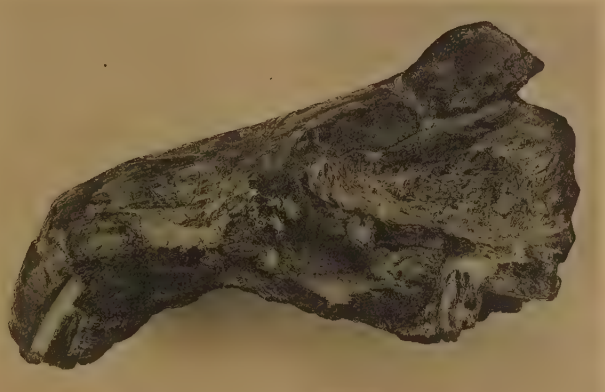

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Tritylodon, Microcleptes.

Plate II.

PLATE II.

PAGE

Tritylodon longaevus Owen 11

Upper Triassic, Thaba N'chou, Basutoland.

FIG. 1.—Crown view of right cheek-teeth. × 3 diam. Brit. Mus. M 1951.

Microcleptes fissurae, sp. nov. 60

Rhaetic, Holwell, Somerset.

FIG. 2.—Crown view of cheek-tooth. × 20 diam. Brit. Mus. M 2401A.

FIG. 3.—Slightly oblique crown view of cheek-tooth. × 20 diam. Brit. Mus. M 2401B.

Thomasia anglica, sp. nov. 66

Rhaetic, Holwell, Somerset.

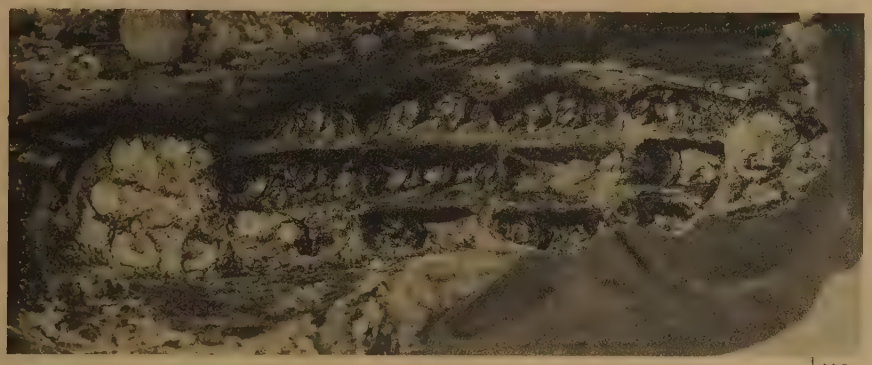
FIG. 4.—Crown view of cheek-tooth: stereoscopic. × 20 diam. Yale Peabody Museum 13622B.

Plagiaulax becklesii Falconer 33

Middle Purbeck, Swanage, Dorset.

FIG. 5.—External view of incomplete left mandibular ramus. × 4 diam. Brit. Mus. 47728.

FIG. 6.—Internal view of fragment of right mandibular ramus with M_{1-2}. × 6 diam. Brit. Mus. 47733.



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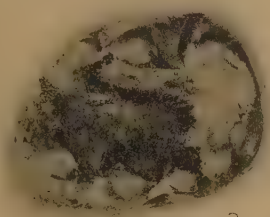

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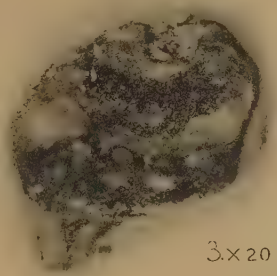

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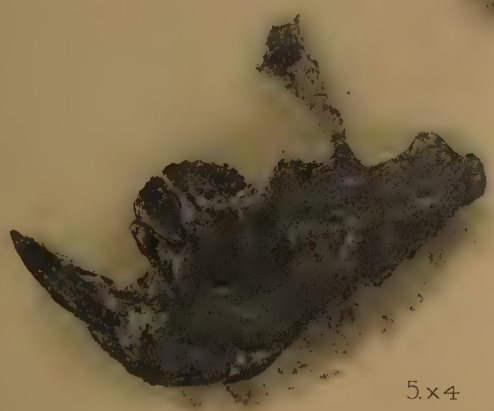

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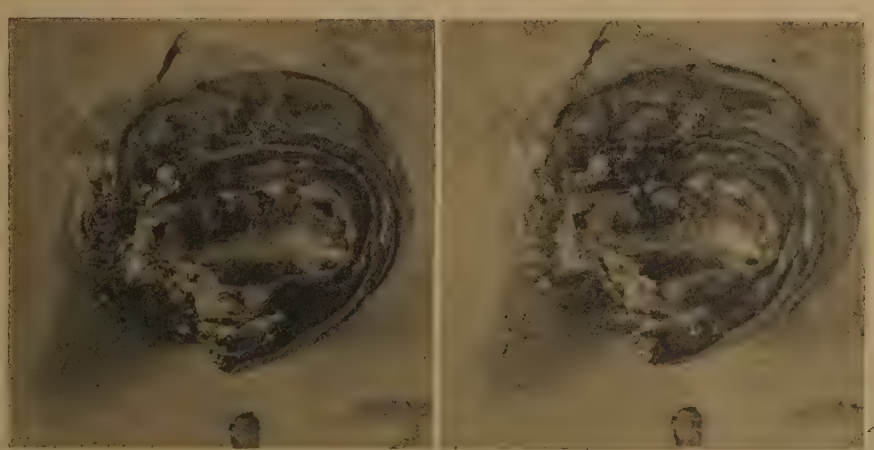

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Tritylodon, Microcleptes,
Thomasia, Plagiaulax.

PLATE III.

PAGE

Plagiaulax becklesii Falconer 33

Middle Purbeck, Swanage, Dorset.

FIG. 1.—Anterior part of right mandibular ramus, external view. × 4 diam. HOLOTYPE. Brit. Mus. 47731.

FIG. 2.—Posterior part of same specimen, internal view. × 4 diam.

Ctenacodon falconeri (Owen) 41

Middle Purbeck, Swanage, Dorset.

FIG. 3.—Anterior part of right mandibular ramus, external view. × 4 diam. HOLOTYPE. Brit. Mus. 47730.

Ctenacodon minor (Falconer) 38

Middle Purbeck, Swanage, Dorset.

FIG. 4.—Incomplete right mandibular ramus, external view. × 6 diam. HOLOTYPE. Brit. Mus. 47729.

Ctenacodon cf. *minor* (Falconer) 40

Middle Purbeck, Swanage, Dorset.

FIG. 5.—Incomplete left mandibular ramus, external view. × 6 diam. Brit. Mus. 48399.

Bolodon osborni, sp. nov. 45

Middle Purbeck, Swanage, Dorset.

FIG. 6.—Right maxilla, external view. × 6 diam. HOLOTYPE. Brit. Mus. 47735A.

Bolodon crassidens Owen 43

Middle Purbeck, Swanage, Dorset.

FIG. 7.—Right premaxilla and maxilla, external view. × 6 diam. HOLOTYPE. Brit. Mus. 47735.

Bolodon elongatus, sp. nov. 48

Middle Purbeck, Swanage, Dorset.

FIG. 8.—Incomplete palate with premolars, the latter seen from the left side. × 6 diam. HOLOTYPE. Brit. Mus. 47736.

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Plagiaulax, Ctenacodon,
Bolodon.

Plate IV.

PLATE IV.

PAGE

Phascolotherium bucklandi (Broderip) 73

Stonesfield Slate, Stonesfield, Oxfordshire.

FIG. 1.—Right mandibular ramus, internal view. × 4 diam. HOLOTYPE. Brit. Mus. 112.

Triconodon mordax Owen 77

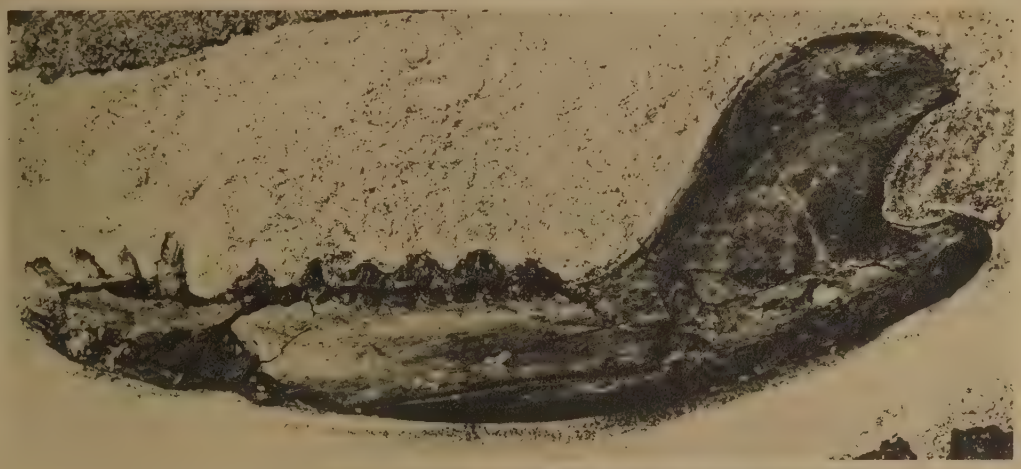
Middle Purbeck, Swanage, Dorset.

FIG. 2.—Left mandibular ramus, external view. × 4 diam. HOLOTYPE. Brit. Mus. 47764.

FIG. 3.—Right lower molars, internal view. × 5 diam. Brit. Mus. 47771.

FIG. 4.—Left M^{2-3}, external view. × 5 diam. Brit. Mus. 47806.

FIG. 5.—Anterior part of left mandibular ramus, external view. × 4 diam. Brit. Mus. 47763.



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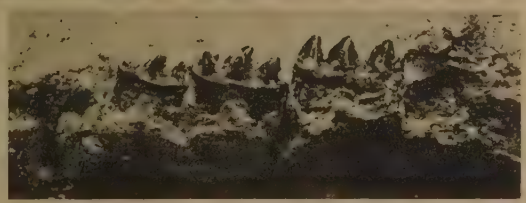

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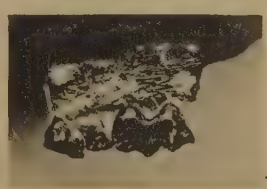

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Phascolotherium, Triconodon.

PLATE V.

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Triconodon mordax Owen 77

Middle Purbeck, Swanage, Dorset.

FIG. 1.—Right parietal and internal mould of left parietal viewed from above. × 3 diam. Brit, Mus. 47763.

FIG. 2.—Left frontal, viewed from below. × 3 diam. Brit. Mus. 47763.

FIG. 3.—Incomplete left mandibular ramus, internal view. × 4 diam. Brit. Mus. 48395.

FIG. 4.—Right M^{3-4}, external view. × 5 diam. Brit. Mus. 48396.

FIG. 5.—Incomplete right maxilla, external view. × 6 diam. Brit. Mus. 47784.

Trioracodon ferox (Owen) 89

Middle Purbeck, Swanage, Dorset.

FIG. 6.—Left mandibular ramus, internal view. × 3 diam. HOLOTYPE. Brit. Mus. 47775.

FIG. 7.—Incomplete left mandibular ramus, external view. × 4 diam. Brit. Mus. 47765.

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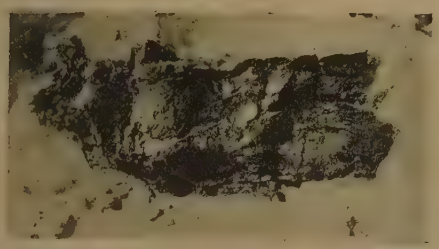

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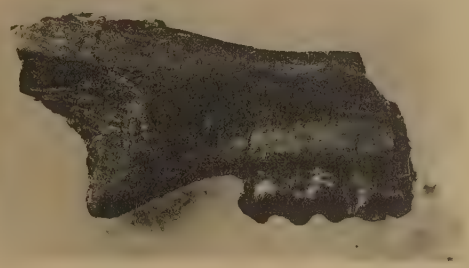

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Triconodon, Trioracodon.

Plate VI.

PLATE VI.

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Trioracodon ferox (Owen) 89

Middle Purbeck, Swanage, Dorset.

FIG. 1.—Right upper canine and premolars, internal view. × 4 diam. Brit. Mus. 47788.

FIG. 2.—Associated mandibular rami. × 3 diam. Brit. Mus. 47782.

FIG. 3.—Incomplete left maxilla, external view. × 4 diam. Brit. Mus. 47779.

FIG. 4.—Incomplete left maxilla, external view. × 3 diam. Brit. Mus. 47774.

FIG. 5.—Incomplete right maxilla, internal view. × 3 diam. Brit. Mus. 47778.

FIG. 6.—Right maxilla, internal view. × 4 diam. Brit. Mus. M 10474.

Trioracodon oweni, sp. nov. 95

Middle Purbeck, Swanage, Dorset.

FIG. 7.—Incomplete right mandibular ramus, internal view. × 4 diam. HOLOTYPE. Brit. Mus. 47766.

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Trioracodon.

Plate VII.

PLATE VII.

PAGE

Trioracodon major (Owen) 96

Middle Purbeck, Swanage, Dorset.

FIG. 1.—Incomplete right mandibular ramus, external view. × 2 diam. HOLOTYPE. Brit. Mus. 40722.

Spalacotherium tricuspidens Owen 99

Middle Purbeck, Swanage, Dorset.

FIG. 2.—Part of left mandibular ramus, external view. × 4 diam. HOLOTYPE. Brit. Mus. 46019.

FIG. 3.—Part of right mandibular ramus, external view. × 4 diam. Brit. Mus. 47749A.

FIG. 4.—Posterior part of left mandibular ramus, internal view. × 5 diam. Brit. Mus. 47750.

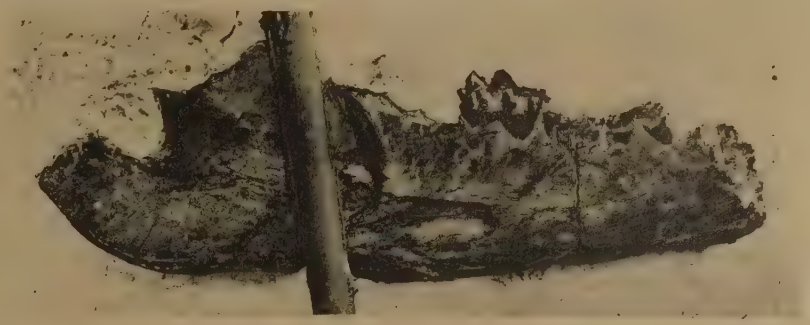
FIG. 5.—Part of left mandibular ramus, internal view. × 4 diam. Brit. Mus. M 5633.

FIG. 6.—Fragment of same jaw as in Fig. 3, with last premolars in internal view. × 4 diam. Brit. Mus. 47749B.

Peralestes longirostris Owen 104

Middle Purbeck, Swanage, Dorset.

FIG. 7.—Incomplete right premaxilla and maxilla, external view. × 6 diam. HOLOTYPE. Brit. Mus. 47740.



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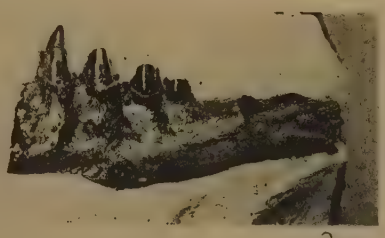

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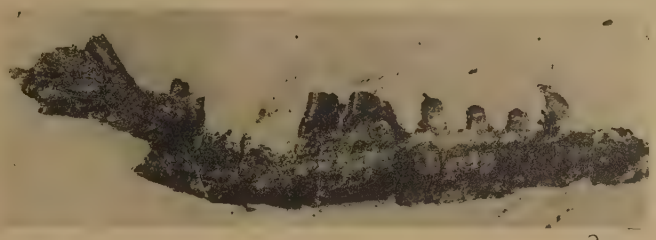

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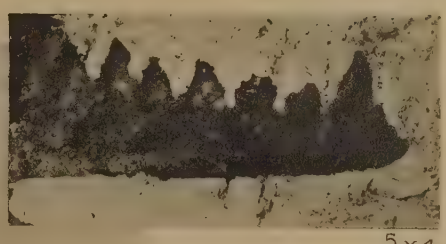

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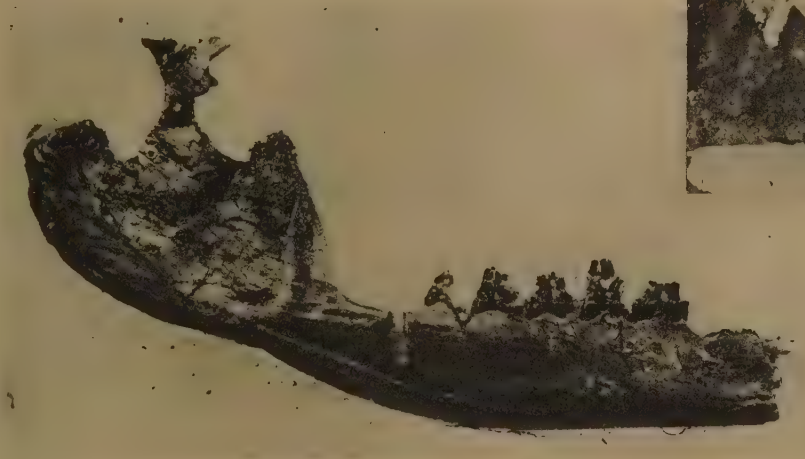

4. x 5

6. x 4

7. x 6

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Trioracodon, Spalacotherium,
Peralestes.

PLATE VIII.

PAGE

Amphitherium prevostii (v. Meyer) 114

Stonesfield Slate, Stonesfield, Oxfordshire.

FIG 1.—Part of right mandibular ramus, internal view. × 8 diam. Brit. Mus. 36822.

Peramus tenuirostris Owen 121

Middle Purbeck, Swanage, Dorset.

FIG. 2.—Left mandibular ramus with anterior end, tip of coronoid process, and angular process broken off, external view. × 6 diam. HOLOTYPE. Brit. Mus. 47742.

FIG. 3.—Part of left mandibular ramus, external view. × 6 diam. Brit. Mus. 47744.

FIG. 4.—Part of left mandibular ramus with complete cheek tooth series, external view. × 6 diam. Brit. Mus. 47739.

FIG. 5.—Part of right mandibular ramus, internal view. × 6 diam. Brit. Mus. 48404.

FIG. 6.—Part of left mandibular ramus, internal view. × 6 diam. Brit. Mus. 47751.

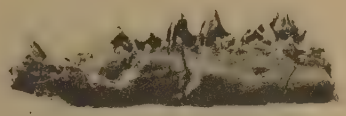
Peraiocynodon inexpectatus, gen. et sp. nov. 126

Middle Purbeck, Swanage, Dorset.

FIG. 7.—Posterior part of left ramus with the coronoid process broken off, external view. × 6 diam. HOLOTYPE. Brit. Mus. 48248.

FIG. 8.—The same, internal view of the molars. × 6 diam.

1. × 8



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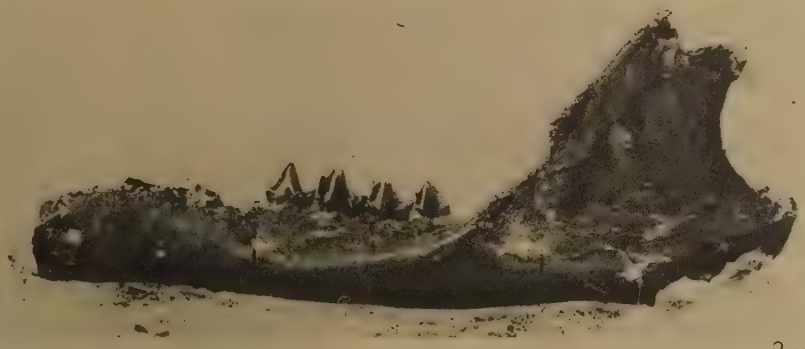

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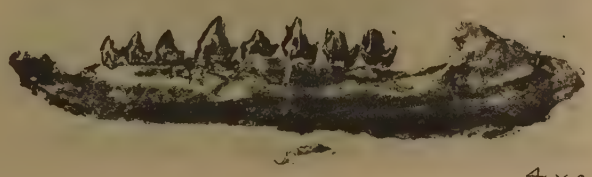

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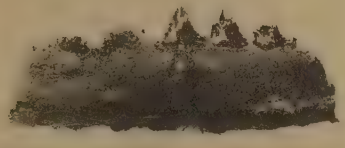

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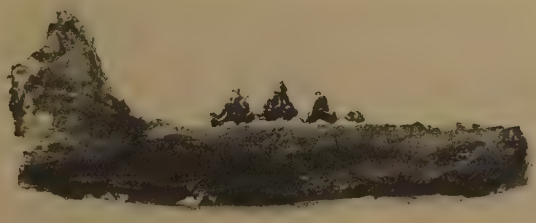

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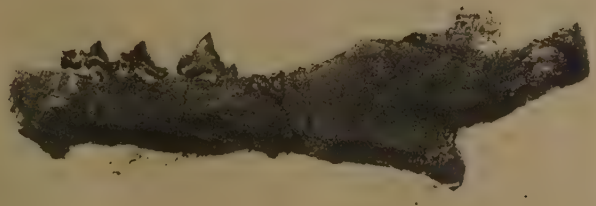

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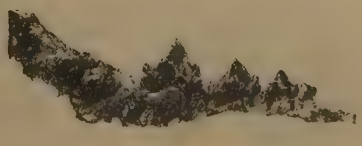

8. × 6

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Amphitherium, Peramus,
Peraiocynodon.

PLATE IX.

PAGE

Amblotherium pusillum (Owen) 130

Middle Purbeck, Swanage, Dorset.

FIG. 1.—Right mandibular ramus, internal view. × 6 diam. HOLOTYPE. Brit. Mus. 47752.

FIG. 2.—Anterior part of left mandibular ramus, external view. × 6 diam. Brit. Mus. 47757.

FIG. 3.—Parts of right and left mandibular rami and of right maxilla. × 6 diam. Brit. Mus. 47756.

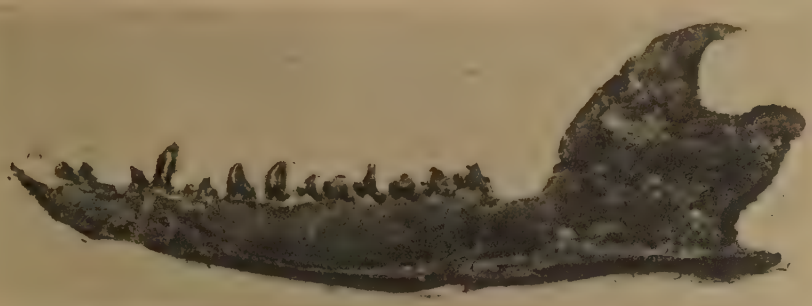
FIG. 4.—Incomplete right maxilla, external view. × 6 diam. Brit. Mus. 47802.

FIG. 5.—Incomplete left mandibular ramus, internal view. × 6 diam. Brit. Mus. 47783.

FIG. 6.—Incomplete left mandibular ramus, internal view. × 6 diam. Brit. Mus. M 10927.

FIG. 7.—Incomplete left mandibular ramus, external view. × 6 diam. Brit. Mus. 47761.

FIG. 8.—Incomplete left mandibular ramus, external view. × 6 diam. Brit. Mus. M 5632.



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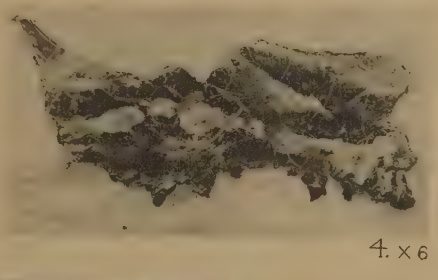
2. x 6

3. x 6



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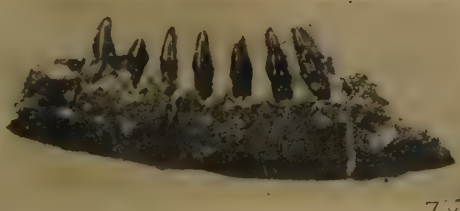
6. x 6



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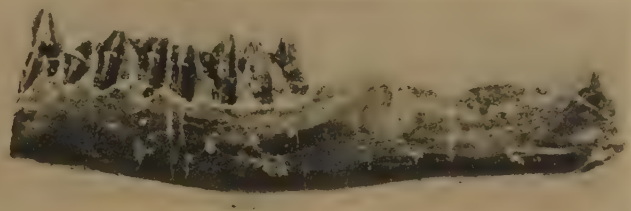

8. x 6

H G Herring photo

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Amblotherium.

PLATE X.

PAGE

Amblotherium nanum (Owen) 135

Middle Purbeck, Swanage, Dorset.

FIG. 1.—Incomplete right mandibular ramus, internal view. × 6 diam. HOLOTYPE. Brit. Mus. 47745.

FIG. 2.—Incomplete left mandibular ramus, external view. × 6 diam. Brit. Mus. 47760.

FIG. 3.—Badly crushed skull with lower jaws, viewed from below. × 4 diam. Brit. Mus. 47758.

FIG. 4.—Fragmentary and crushed vertebral column associated with the skull seen in Fig. 3. × 4 diam. Brit. Mus. 47758.

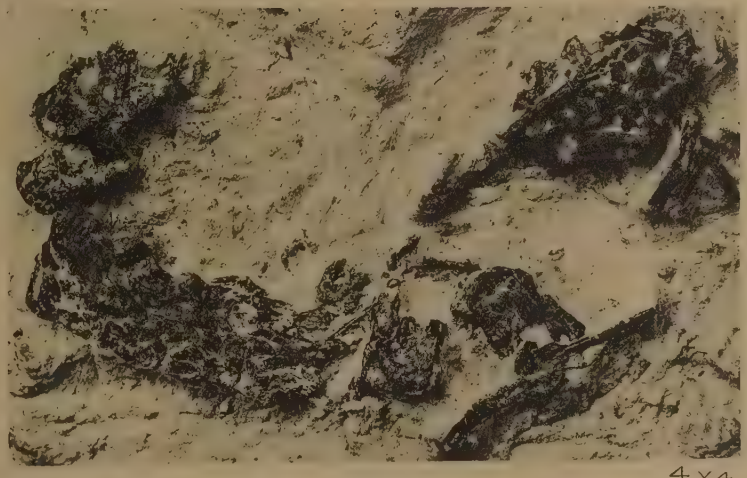
FIG. 5.—Incomplete left ramus, internal view. × 6 diam. Brit. Mus. 47785.

FIG. 6.—Right maxilla with last two premolars and M^{1-7}, palatal view. × 8 diam. Brit. Mus. 47786.

1. x 6

2. x 6

3. x 4



4. x 4

5. x 6

6. x 8

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Amblotherium.

Plate XI.

PLATE XI.

PAGE

Kurtodon pusillus Osborn 140

Middle Purbeck, Swanage, Dorset.

FIG. 1.—Incomplete left maxilla with teeth, internal view. × 6 diam. HOLOTYPE. Brit. Mus. 47755.

FIG. 2.—Same, crown view. × 6 diam.

Peraspalax talpoides Owen 142

Middle Purbeck, Swanage, Dorset.

FIG. 3.—Part of left mandibular ramus, internal view. × 6 diam. HOLOTYPE. Brit. Mus. 47738.

Phascolestes mustelula Owen 143

Middle Purbeck, Swanage, Dorset.

FIG. 4.—Anterior part of left mandibular ramus, internal view. × 5 diam. Brit. Mus. 47741.

FIG. 5.—Right mandibular ramus, internal view. × 4 diam. HOLOTYPE. Brit. Mus. 47753.

FIG. 6.—Incomplete right mandibular ramus, internal view. × 4 diam. Brit. Mus. 47808.

Dryolestidae Incertae Sedis 145

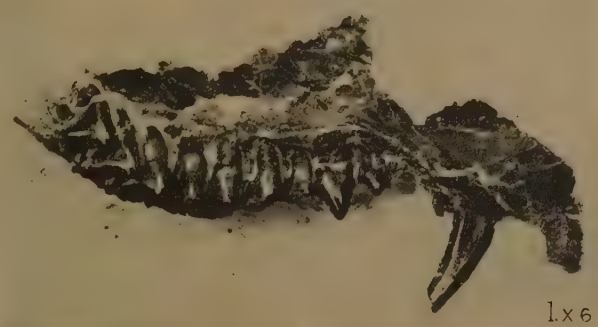
Middle Purbeck, Swanage, Dorset.

FIG. 7.—Part of left mandibular ramus, external view. × 6 diam. Brit. Mus. 48405.

Pantotheria Incertae Sedis 146

Middle Purbeck, Swanage, Dorset.

FIG. 8.—Upper (?) canine. × 4 diam. Brit. Mus. 48208A.



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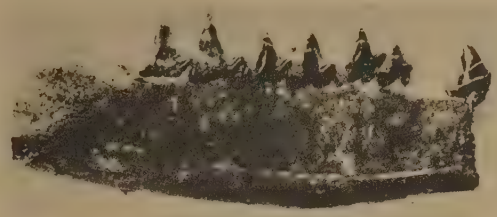

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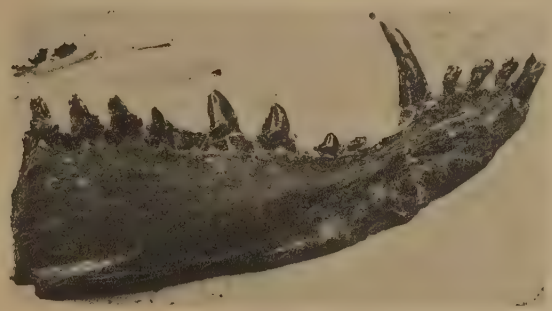

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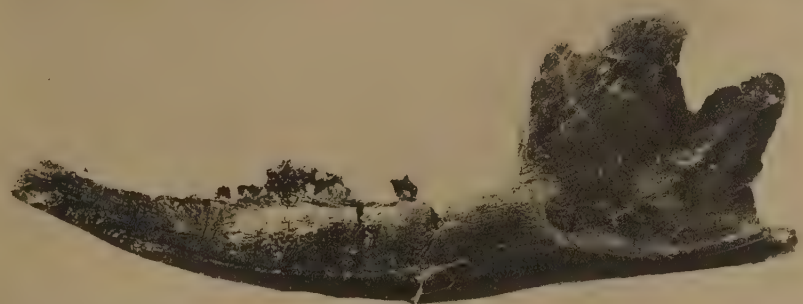

5. x 4

6. x 4

7. x 6

8. x 4

H. G. Herring photo

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Kurtodon, Peraspalax,
Phascolestes, Incertae,
Sedis.

PLATE XII.

PAGE

Eodelphis cutleri (Smith Woodward) 148

Belly River Formation, Alberta, Canada.

FIG. 1.—Incomplete right mandibular ramus, external view. × 2 diam. HOLOTYPE. Brit. Mus. M 11532.

FIG. 2.—Same, crown view. × 2 diam.

FIG. 3.—Same, internal view. × 2 diam.

Mammalia Incertae Sedis 149–160

Stonesfield Slate, Stonesfield, Oxfordshire.

FIG. 4.—Right humerus, posterior view. × 3 diam. Brit. Mus. M 13127.

FIG. 5.—Right femur, posterior view. × 3 diam. Brit. Mus. 32752.

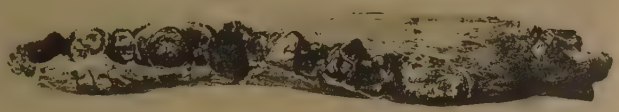
Middle Purbeck, Swanage, Dorset.

FIG. 6.—Right femur, posterior view. × 3 diam. Brit. Mus. M 13126.

FIG. 7.—Right femur, anterior view. × 3 diam. Brit. Mus. 48250.

FIG. 8.—Incomplete left humerus and fragment of radius. × 3 diam. Brit. Mus. 48361.

1. x 2



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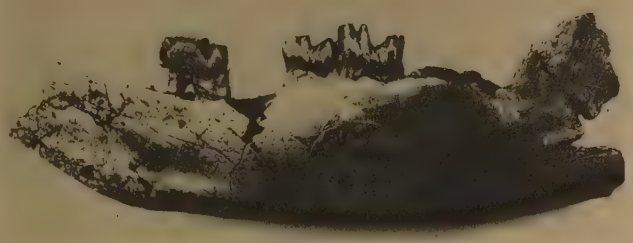

3. x 2

6. x 3

7. x 3

8. x 3

4. x 3

5. x 3

H. G. Herring photo

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Eodelphis, Incertae, Sedis.

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